# THE METHOD OF EVOLUTION

A REVIEW OF THE PRESENT ATTITUDE OF SCIENCE TOWARD THE QUESTION OF THE LAWS AND FORCES WHICH HAVE BROUGHT ABOUT THE ORIGIN OF SPECIES

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# PREFACE

IT is becoming evident that the future investigation of the problem of Evolution must be by new men. Nearly all who undertook the study of the subject under the stimulus of the early writings of Darwin have passed away, or are beyond the age when they may be expected to carry the discussion into new fields. Even a later generation that contributed largely to the moulding of our ideas is also beyond the age when we may expect from them much in the way of advance for the future. The discussion must hereafter be in the hands of a generation of scientists whose first introduction into science found it illumined by the light of evolution, and who have not been obliged to convince themselves of the truth of the conception. We may feel sure that we have seen the last of the contributions to this subject which will come from the older group of scientists, and in the future must look for new minds to take the legacies which have been handed down, using them as foundation stones upon which to build a more consistent whole.

The evolution discussion of the forty years follow-

ing Darwin has been largely one of deductive science. The formulation of the law of natural selection started an immense amount of speculation as to how it might act and what it would produce under certain conditions. A very large part of the discussion is such as might be drawn directly from the law itself without any special appeal to nature for information. The younger naturalists are expressing themselves as dissatisfied with this method of study, insisting that if we are to advance any further in the subject it must be by inductive methods rather than deductive. We must leave our libraries and turn to nature to see what is actually going on, leave speculation and turn to observation. A new era in the evolution discussion is coming with new men. The younger naturalists are beginning to hunt in new fields rather than in those already well explored, and we may expect the aspect of the problem to be greatly changed as the result of this new attitude.

The last fifteen years have seen a very profound modification of our ideas concerning the origin of species, but the facts that have produced the change have hardly been within the reach of the person who is interested in evolution but cannot follow the discussion in its various ramifications in scientific journals. The purpose of this work is to present to such students a review of the subject of evolution as it stands to-day, at the time when our younger naturalists are abandoning old methods and beginning to search in new fields for new information.

One of the most significant fields of the application of evolutionary methods of study is that of

mental phenomena, including the study of instinct and intelligence, together with the evolution of civilization. The limits of this work make it impossible to deal with this most important subject, which must, therefore, be reserved for a later work.

MIDDLETOWN, August, 1899.

NOTE.—Figures 8, 10, 11, and 13-24 are from the author's *Story of the Living Machine*, and have been loaned by D. Appleton & Co.

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# THE METHOD OF EVOLUTION

## CHAPTER I

### INTRODUCTION

IT is the boast of science that it is guided by evidence and not by speculation. It is equally true that there is no branch of science whose advance has not been largely dominated by theories which extend much beyond demonstrated fact. Science is to-day dominated by the idea of evolution. The change that has been produced in our methods of thought by the spirit of evolution can only be realized by a comparison of the philosophy of the first half of the century with that of to-day.

If one attempt to contrast the spirit of the earlier with recent thought one might aptly say that while formerly nature was studied as *at rest*, to-day it is studied as *in motion*. While it was then studied as something that had been created and only needed analysis, now it is studied as something constantly

being created and as constantly producing new conditions. Attention has been turned from the question of what exists to the question of how it came to exist. The quest for truth has ceased hunting for facts and is looking for laws. We are no longer content to discover a butterfly, name it and put it in a museum as a zoölogical specimen, but we must ask how it got its beautiful colors. We are no longer content to analyze the faculties of mind, but are constantly asking how the brain came to have these faculties, and what has been the history of their development. We have ceased to be content with the study of things at rest, but must study them as in motion and as parts of an endless flow of creation.

The ideas which are comprised under the general term evolution did not originate with Darwin nor indeed with this century. On the other hand, while some general notion of an evolution may be traced back to the Greeks it is a mistake to conceive these ancient philosophers as having any ideas similar to those of modern evolution. Their thoughts were full of mysticism. They had little knowledge of nature and found it full of insoluble problems. Early man had a direct consciousness of personal volition, and he learned to explain the mysterious phenomena of nature as the direct action of some supernatural beings. He created an unseen world to explain what is seen. A phenomenon that was unintelligible to him was at once shrouded in mysticism. But the very essence of modern evolution is the explanation of all natural phenomena by the action of natural laws, and in such a thought there

is no room for mysticism, except indeed the mysticism of natural law itself.

### *Modern Era of Thought*

The beginning of our modern era of thought, which has led to a definitely formulated doctrine of evolution, occurred at the time when philosophers first began to substitute natural force for mysticism. It is of course hardly possible to state very closely when this new era began. One of the greatest early steps in this direction was the formulation of the law of gravitation. It was natural that the reign of law should be first perceived in that realm of nature where the facts are simplest, and astronomical phenomena, although complex indeed, are simple enough compared with the phenomena upon the earth's surface. The former are capable of mathematical formulation; the latter must ever baffle mathematics. Newton succeeded in showing that the motions of the heavenly bodies are controlled by the simple law of gravitation, and that there is no more mystery about them than there is in the fall of a stone to the ground.

There soon followed the development of the same general line of thought in other departments of nature. Physical and chemical problems were studied, and slowly the miscellaneous unintelligible phenomena of the physical universe were reduced to order and comprised under the realm of law. The mysticism of fire and lightning were replaced by the laws of oxidation and electricity. While we do not usually look upon these sciences as belonging

to the doctrine of evolution they are in reality integral parts of it since they represent the general substitution of natural forces for supernatural. When finally these sciences culminated in the doctrine of the conservation of energy there was furnished the foundation upon which the new philosophy of the origin of nature could be built.

The next step in the general advance was the application of the newly discovered laws of physical nature to the interpretation of the condition of the earth's surface. The fact that the earth has had a history became clear as the rocks were studied, and the interpretation of that history then demanded attention. The action of the forces of chemistry and physics gave the key to the problem. It soon appeared that the explanation of the present condition of the earth's surface is to be found in the constant action, during past ages, of the forces now in operation. To explain mountains and valleys, rocks and sands, and even volcanoes and fossils, are needed no new forces. The world was not created in its present form, but it has slowly grown into the present condition, and the efficient powers which have brought about this growth are the very ones which the last two centuries have been investigating. There was thus presented to the philosopher the new problem of tracing this world-history and finding out to what extent the forces now acting are sufficient to explain the earth's crust. This has been the task of the geologist, and from the fourth decade of the century the endeavor to explain the world of to-day as the result of known forces acting

upon the world of yesterday has been the foundation of geology. More and more clearly, as the century has advanced, has it appeared that geological phenomena have all been controlled by law, and that, beginning with a molten sphere, which astronomy has offered science as a starting-point, the present globe with its diversity of surface has resulted from the action of exactly the same forces of heat, shrinking, and erosion which we see in play on all sides of us to-day. Astronomical evolution starts with the nebula and produces the solar system. Geological evolution starts with a molten fragment of this system and produces the world; and the essence of the whole is that all this has been the result of inherent forces; by which is meant simply what we call natural rather than supernatural forces.

The application of this reign of law becomes more difficult as the phenomena to be explained become more complex. There is still another realm of nature far more complex than geology. The phenomena connected with life present an endless series of new problems. Life is active, rocks are inert. Living things seem to be guided by internal forces, the mountains are formed by external forces acting upon the rocks. Living things are adapted to conditions in a wonderful manner; adaptation of part to part for a definite purpose does not occur in lifeless nature. Law and force are blind and may well explain the meaningless series of hills and valleys, but how can they explain such a delicately adjusted mechanism as the eye? In our experience intelligence is always necessary to contrive a mechanism.

## *Organic Evolution*

But it was inevitable that the onward sweep of thought should include life phenomena in the reign of law. Science saw before it the task of explaining nature. With inanimate nature yielding to the reign of law the necessity for solving animate nature became more pressing. For even if the geologist were completely successful the search for nature's secret were futile if living phenomena remained unexplained. The problem of the origin of animals and plants became, therefore, a final goal of research. If it could be shown that living phenomena were also produced in accordance with known forces the whole universe would become luminous under the reign of law. But if living things should refuse to be thus accounted for, if they should persist in remaining isolated creative fiats, the whole structure of evolution built upon the idea of law would fall to pieces. Hence the problem of organic evolution becomes the great problem. As this question is settled so will be settled the whole of the far-reaching doctrine of evolution. Deny the evolution of living things and nothing is left of the reign of law except meaningless fragments. Grant that animals and plants have come into existence as the results of natural law and the whole of the far-reaching doctrine of evolution may follow.

While this is the logical relation of the problem of *organic* evolution and *philosophical* evolution it has not been their chronological relation. The conception of philosophical evolution as it exists

to-day has grown out of the belief in the evolution of life rather than the reverse. For a long time the term evolution was to most persons synonymous with the idea of organic evolution, the broader aspects of the problem being overlooked. The term evolution is certainly much broader than the simple problem of the origin of animals and plants. At the same time it is so evident that organic evolution forms the keystone of the evolutionary arch, without which it would fall to pieces that the whole debate has for years centred around the problems of organic evolution.

In the last forty years of the century biological investigation has been devoted to studying the question whether the reign of law applies to the origin of the different species of animals and plants, and in trying to find out whether natural forces are sufficient to explain animate as well as inanimate nature. It cannot be claimed that the question is fully answered. Some of its problems have been solved with certainty. Enough light has been thrown upon the subject to convince scientists that the final outcome will show that living nature is truly controlled by law and that the making of an animal is just as truly a matter of natural law as the making of a mountain. But we are as yet far from a complete solution. With all our search the essence and origin of life has thus far eluded our grasp. The scientist should go no further than the evidence leads him and should not indulge in too much philosophical speculation. Biological study may have practically demonstrated the evolution of

species but it is far from demonstrating philosophical evolution. If organic evolution had been disproved of course the broader conception of evolution would have fallen; but with the admission of organic evolution as a fact there are still many problems to be solved before the general conception of evolution can be regarded as firmly founded.

### *The Question of Fact*

The question of whether organic evolution is a fact has been sharply before the world now for forty years, and has been studied from many standpoints. Manifestly one of the first questions to be asked upon this subject would be whether the living world has had a continuous history. If evolution is a fact it must follow that the species of to-day have been produced from the species of yesterday as the result of forces acting upon them. If such is the case then the history of species must have been as truly a continuous one as has been the history of the races man. If on the other hand the species of animals and plants have appeared by creative fiats we could expect no such continuous history; or rather there would be no *history* of animals and plants, but only separate histories of individual species.

It is hardly necessary to state that the result of the forty years' study has been to convince science that the doctrine that the present species are descended from those of the past, and these from still older forms, represents the true history of nature.

Although science gives as yet no hint of how the process first started, it has shown to its own satisfaction that, once started, the history of living things has been continuous, one type changing into another until we have the diversified life of to-day, all derived from the species of the past without break. Were the history otherwise, it would be hopeless to try to answer the more seaching question of how the different species have arisen. But when we find that continuity of descent has been the history of life, we may have great hopes that the *method* of descent may be learned. In other words, having learned that the horse as well as the mountain has been produced by slow growth, we may believe that we shall be able to learn *how* natural forces produced the horse, just as we have learned *how* they produced the mountain.

But we must notice that there are two very different questions connected with the evolution problem. The first is the question of *fact* and the second the question of *method.* Confining our attention, as we shall do, wholly to organic evolution, there is first the question whether the history of species has been one of evolution. If we conclude that present species have descended from earlier species, then we must answer the further question of the *method of evolution*, and must learn what laws and forces have been involved in the origin of species. Until we can answer the second question, we cannot feel that we understand nature, howsoever positively we may answer the first.

The distinction of these two questions has not

always been clearly kept. Not a few of those who have been disputing some of the alleged methods of evolution have believed that they were arguing against the fact. Many, who are only partly familiar with science, think that because scientists are still in dispute as to some of the evolutionary theories, therefore evolution itself is still under dispute, and should not be accepted until science has agreed upon its theories. As we shall learn, science is very far from being in agreement in regard to many phases of evolutionary thought, but these matters of disagreement refer to method rather than to fact. We should not let the dispute as to method blind us as to their agreement as to fact. Whatever be their lack of agreement as to the theories of evolution our scientists are agreed to-day with practical unanimity that the theory of descent represents the actual history of the organic world. All modern biological science is based upon this conclusion and it would probably be impossible to find among modern scientists anyone who would venture to hold any other opinion. We must accept this conclusion as settled so far as concerns present day scientists. We find nowhere to-day any thought of discussing this question any more than of discussing the truth of the law of gravitation. We hear less of such discussion than a few years ago, simply because science regards it as beyond discussion and accepts is as a demonstrated conclusion. The evidence that has brought about this conclusion need not be given here. It has come from all departments of biological and geological research, and has led to the

universal belief among biologists and geologists that our modern species of animals and plants have been derived from earlier species by descent.

But the acceptance of this conclusion is far from settling the questions of organic evolution. The aim of the scientist is to *explain* and not simply to *observe*. He tries to turn the question *why* into the question *how*, although frequently as yet unable to do so. After accepting the descent doctrine we have the history only as a matter of sequence—having accepted the origin of species by process of reproduction and descent, but having obtained no knowledge of the forces which have brought about this descent. We have the fact but not the method. The two problems of fact and method have been considered together in the discussions of the last forty years for it is evident that they cannot be separated. Indeed Darwin's contribution to the subject which inaugurated the modern doctrine of evolution was one of method. In the discussions that have followed, the two problems have been becoming more and more distinct. The question of fact has been rendered more and more clear while the question of method has become more and more confused. While upon the question of fact there has been a practical unanimity, it is probably not incorrect to say that upon the question of method there is to-day greater uncertainty of opinion and greater confusion than at any previous time. This is not, however, because we know less of the subject, but because we know more. It is because the problem has not proved to be the simple one at first

conceived, but to have many factors entering into it not at first expected.

It is perfectly clear that the really significant question is rather that of method than fact. The facts in regard to the motions of the heavenly bodies only became significant after the laws governing them were discovered. The history of the earth's strata only acquired a meaning after we learned of the laws and forces that guided that history. So, too, with the origin of species. The facts only acquire a meaning after we learn the laws under which they have been produced. The aim of scientific research in the last centuries has been to find a natural explanation of natural phenomena. The mere fact of the origin of species by descent has comparatively little interest unless it can be shown that the forces which have produced this descent are the same natural forces which are constantly in action around us. Hence the question of method is really the significant one. We may now, then, turn to our immediate subject of the method of evolution, and it will be our purpose in the following pages to consider what we know, and some things that we do not know, in regard to the laws and forces which have brought about this evolution of species.

## CHAPTER II

### THE QUESTION OF METHOD—DARWIN'S SOLUTION

BEYOND a doubt the causal investigation of living phenomena is the most difficult of all problems. Whether it will ever be solved is doubtful, but this is at all events the problem which our biologists are now trying to solve.

Perhaps an example will make our aim clearer. A photograph camera is a mechanism adapted to a certain purpose. In constructing it the laws of optics were considered as well as those of chemistry and mechanics. It was designed for a definite purpose, and being thus designed it fulfils its purpose completely. But the camera did not appear spontaneously, and there are no forces which we know in nature, apart from human intelligence, which could have produced the camera. Under the influence of intelligent design the forces of nature were used to build the camera. But it is not the forces of chemistry nor the laws of optics that explain the existence of the camera. Its existence is explained by the intelligence of man.

Now in the vertebrate eye we have a very similar

mechanism, although one considerably more complicated than the camera. It too is constructed in accordance with the laws of optics and mechanics. It too is a mechanism with a purpose. To fulfil this purpose it has part adapted to part, all acting together in harmony for one end. Now evidence tells us that this eye has been derived from simpler eyes by descent, and that its history has been one of growth and development into its present condition. But manifestly this does not explain the existence of the eye. We know of no forces in the realm of physics or chemistry that are capable of adapting part to part to produce a mechanism, and yet the eye is a mechanism. Natural forces are blind, and do not make machines. We can understand their making mountains, for these are not made of parts adapted to a definite end. The only knowledge of machine building which we have is that of human intelligence. If, therefore, we are to find the method of the origin of species, and thus explain organic evolution, we must discover some force or forces which may fill the place held by human intelligence in the designing of the photographer's camera. The laws of optics and physics no more explain the origin of the eye than they do the origin of the camera. Intelligence explains the adaptation of the parts in the one machine. What accounts for the same phenomena in the other? Every animal and plant is a complicated machine with many parts delicately adapted to act in harmony. Intelligence manipulates natural forces to build a steam engine. What directs these same forces

to build the natural machine which we call the organism?

*The Answer Given by Lamarck*

There are two most obvious differences between the natural machine, the organism, and the artificial machine, the camera. The organism is (1) subject to great changes under the influence of the surroundings, and (2) it reproduces itself. These two factors should furnish our data. At the very beginning of the century Lamarck used them for explaining the origin of species. He depended chiefly upon the first factor, the modification by conditions. As would be expected of a theory arising at this early date, Lamarck's views were more or less mystical: they involved a law that animals had a tendency to increase in size. They contained a somewhat mystical notion that animals could develop organs as the result of effort of their own. But the most prominent feature of Lamarck's theory was that by *use* animals could strengthen any part and increase its size, and that conversely if the part were not used it would diminish in size and efficiency. Such increase and decrease as the result of use and disuse are phenomena familiar to everyone. Lamarck simply assumed that these effects were inherited by subsequent generations, and use and disuse became the great factors in producing the evolution of organs. The theory of Lamarck was in many respects unsatisfactory and incomplete. It gave no explanation of the development of plants

where neither use nor disuse come into play. It made no great impression upon science, and was soon allowed to drop out of sight. In later years it has been revived and we shall notice it again in the proper place.

*The Answer Given by Darwin*

A more comprehensive attempt was made to answer the question by Charles Darwin. His answer depended chiefly upon the second of the factors above mentioned, viz., reproduction. After long and careful investigation he definitely formulated his views into a general theory so well known to-day under the name of Natural Selection. This theory has to-day become almost a part of common knowledge. But inasmuch as all later discussion of the method of evolution is based upon it, it will be necessary for us to present the theory clearly at the outset, even though the subject be familiar to most readers. It may be well to introduce the subject by an illustration.

Imagine that in a certain locality there are two species of butterflies of somewhat the same size, and that one of them is agreeable to the taste of birds while the other is distasteful to them. We may suppose that both are bright colored, the tasteful species, for example, being yellow and the other orange. Imagine now that the distasteful species has a peculiar method of flight, flying in a curved rather than a straight line. A bird that is looking for its breakfast perches itself on a tree and watches

the butterflies that cross a neighboring open space. When he sees a butterfly with the irregular method of flight he pays no attention to it, since he has learned that such butterflies are not pleasant eating. Now the tasteful species of butterfly, like all others, is constantly undergoing variations in many directions. By this we simply mean that the individuals are not all alike, but show all sorts of differences. For instance we may imagine that some of the individuals chance to differ from the normal in their method of flight. If among them there chance to be some that have a method of flight somewhat irregular, and a little like that of the distasteful species, it is evident that the bird will let them alone. The individuals protected by this variation in flight will be likely to reach maturity and produce offspring, while the others without this variation will be devoured by birds. Now if the offspring inherit the characters of their parents it will follow that the next generation will show a larger number of individuals with this new variation. The bird will go on feeding upon the butterflies which show the direct mode of flight, leaving the others alone, and manifestly, after a few generations, the individuals with the old method of flight will be likely to disappear, replaced by the new type.

But now the bird finds its food becoming scarce, and from his perch on the tree he sees none but the irregular-flying butterflies. This forces him to hunt more carefully, and he finally discovers, possibly by accident, that some of the irregular-flying butterflies are yellow and others orange, and that the yellow

ones have a pleasant taste. From this discovery he will learn to take notice of the color as well as the method of flight, and an irregular flight will no longer be a protection. But variations in color are occurring among the animals as well as variations in method of flight. We may suppose that among the tasteful species some individuals have a little red mixed with the yellow pigment, giving them an orange hue. Evidently now these individuals will be protected and the yellow ones alone fall prey to the bird's appetite. This selection will thus gradually increase the number of orange-colored individuals. Again the bird will find his prey becoming scarce, so that he is forced to hunt more sharply. Perhaps he next discovers that the distasteful species has some dark spots on the wings while the other species is plain. His choice will now be guided by this fact. But variations continue at all times and in all directions. Amid the hundreds of thousands of individuals of the agreeable species it is pretty certain that some will vary in such a way as to show some dark spots. If such a variation occurs it is evident that these individuals will be rejected by the bird, the others being eaten, until the spotted individuals displace the plain-colored ones. And thus the process goes on. By the selection in each generation of the individuals best fitted to escape the attention of the bird, or more strictly by the death of the individuals least fitted to escape attention, change after change will be produced. The agreeable butterfly will become more and more like the distasteful one until it requires the very closest

attention on the part of the bird to distinguish between them.

While this illustration is largely imaginary, since no one has actually seen the production of such characters, it is well known that just such instances of mimicry occur among butterflies, and it certainly seems that the explanation given accounts for their origin without any recourse to intelligent design. Of course the development of such mimicry will not take place unless the right variation should occur at the right moment. It may appear a rare chance, for example, that these butterflies should have become orange at just the right time. Why should they have become orange instead of red or green? The answer is that variations in color of all kinds do constantly occur. Ordinarily such variations mean nothing to the species since they furnish no protection. They are like the waves of the sea ever coming and going without leaving a trace. Orange variations occurring when they did brought about the preservation of such individuals as were fortunate enough to show them, since they afforded a protection which the yellow individuals lacked.

This example will serve to illustrate the forces in nature which Darwin combined into the theory of natural selection. This theory consists of a chain of five links, each of which is fundamental to the theory. These five links are, moreover, not only fundamental to the theory of natural selection, but, as we shall see, they lie at the bottom of all attempts to determine the method of evolution, whether in accordance with the views of Darwin or

of the later scientists who have tried to solve the problem. We must therefore at the outset learn what these five links are. They are as follows:

1. *The Prodigality of Nature.*—Reproduction is a universal phenomenon of living things, and is manifestly the basis of organic evolution, since it is the chief point where the natural machine differs from the artificial. A striking factor of reproduction is that it appears to be far more rapid than is necessary. All animals and plants seem to multiply much more rapidly than is needed to preserve the species. Where there is food enough for a single individual perhaps hundreds are produced. Bacteria multiply so rapidly that only a week would be required to fill the world with descendants of a single individual if they were to multiply unchecked. A bird producing two offspring in a year would in twenty years have a million descendants; and even the slow-breeding elephant would in the course of seven hundred and fifty years have thirteen million descendants; a rate of multiplication absolutely incompatible with the possibilities of existence. Births vastly outnumber the individuals that reach maturity. It follows, of course, that the vast majority must die without being able to produce offspring. This leads to the second link of the chain.

2. *Struggle for Existence.*—From the moment of birth, nay, from the moment that the egg is produced by the mother, these numerous offspring are thrown into competition with each other. From the outset of life the progeny begins to be weeded out. Almost infinite are the factors in this compe-

tition for life. In some cases the egg is not fertilized. In others the egg is swallowed as food, or the young helpless larvæ are eaten by enemies. During the period of growth from the egg to the adult this extermination goes on. The young find it too hot, or too dry, or too wet; they fail to find proper food; they are attacked by parasites or larger enemies. Day after day this weeding out continues, and, by the time that maturity is reached, there may be only a few of the original brood left alive. But even with maturity the competition is not ended. The adults have similar problems. They have combats with each other, sometimes active combats, but more often purely passive ones in search for food. They have numerous enemies to avoid, and the individual that is able to pass through all dangers of its early life and finally obtain a mate so that its eggs can be fertilized and produce offspring, is the very decided exception.

All this is called the *struggle for existence*, a term that is sometimes misunderstood and thought to indicate an actual struggle of individual with individual. It really means, however, simply the endeavor of each individual to obtain food and a chance to live. Two seeds that fall side by side upon a plot of ground where there is room enough for only one plant have just as truly a struggle for existence with each other as have two tigers fighting for a carcass. Each of the seeds sends its roots into the ground, and each tries to get a foothold in the ground in advance of the other. It is of course a purely unconscious struggle, but it is just as truly

a struggle for existence as can be found among the fiercest animals when fighting with each other to the death. Indeed, the struggle for existence in organic nature is usually of this purely passive character.

3. *Variation.*—Even a cursory study of animals and plants shows that they are not all alike. The children of the same parents differ from each other, and, when the offspring of different parents of the same species are compared, the differences are found to be universal. It is probably impossible to find two individuals of any species of animals or plants that are exactly alike. Why there should be these differences among individuals of the same species is a question to be raised later. At present we are only concerned in the fact that such variations are universal.

4. *Survival of the Fittest.*—The question as to which of the numerous competing individuals shall survive is a vital one for the species. If the individuals were all alike it would of course be simply a matter of chance as to which would reach maturity. Under any circumstances it must be recognized that the survival will be largely a matter of accident. But the existence of variations on every hand makes it no longer a matter of mere chance, and brings about a law of survival. If there are among the hundreds of individuals some that are less adapted to the conditions than others, these will be the ones to yield in the struggle, and die without producing offspring. If, on the other hand, there be among the variations some which render their possessors better adapted to their conditions

these animals will be the ones to survive the struggle and produce offspring. This is the *survival of the fittest*, or *natural selection* in a narrower sense.

In order to understand this link in Darwin's chain it is, however, necessary to understand what is meant by the fittest. It means simply the individual that is best adapted to its conditions of life. It does not always mean the strongest, for sometimes the strong individuals may do battle with an enemy while the weaker take the opportunity of consuming the food. It does not always mean the largest, for the smaller individual needs less food and may survive a period of famine that would destroy the larger individual who demands more food. It does not always mean the most highly developed, for it may be an advantage to an individual to lose some of its organs, as, for example, when it becomes a parasite. It may mean the largest, or the smallest, the animals with the longest or the shortest toes, the plant with the largest or the smallest leaves. It may mean the shrewdest or the stupidest individual. In all cases, however, it does mean the animal that is best adapted to the conditions in which it lives. The acquirement of a new habit. the adoption of a new food plant, a change in colo all such things are factors in determining which o number of individuals contending for food wil the ones most likely to get it, and therefore victors in the struggle for existence. The " fit will constantly change with changing cond and that which is fittest to-day may not be morrow under new circumstances.

5. *Heredity.*—It is a well recognized fact that offspring inherit the characters of their parents. This general statement may be made without any danger of contradiction, although the matter must be more closely analyzed later. From this it will follow that the offspring of individuals who have survived the struggle will have a tendency to inherit the characters of their parents. These parents, however, have survived because in some respect they were better adapted to the conditions of life than their competitors. From the fact of heredity it will follow that the individuals of the next generation, since they have all descended from parents endowed with some special advantage, will have a tendency to inherit the favorable variations which their parents possessed. In this next generation, therefore, there will be many individuals with the same advantage which the survivors of the last generation possessed. They will all be thus better fitted for existence than the average individuals of the last generation. As a result a few generations would see complete extermination of those without this variation and the survival only of such as possessed the character in question. Thus a peculiarty, which appeared at first as an accidental variation, 'll be in time possessed by *all* survivors. After individuals of the race have acquired this pecuty it is plain that it will be of no particular to any one of them, so that the survivor in ruggle must now be determined by some other But since variations appear constantly, ıer variation will soon give its possessors an

advantage. Some of the individuals may show the original peculiarity better developed, or perhaps something entirely new. This new variation will have its influence, and in time drive out of existence all animals in which it is less favorably developed. And so the process would be repeated over and over again, each generation adding something to the sum total, and the race undergoing a slow change. Natural selection is thus a force ever watching for some variation which may be of use. Unless variation appears, selection is powerless; but since variations are constant, it will happen that when favorable variations do appear they will be "seized upon by natural selection" and "fixed" as race characters.

*Origin of an Eye as an Illustration of Natural Selection*

Natural selection can only explain the origin of a mechanism when it can be shown that it has been produced by successive steps. If a complicated organ should appear at one single step then natural selection would not explain it at all. Natural selection shows how little steps may be added to each other until complicated organs result. If it can be shown that the mechanisms have been slowly produced by many separate stages, each of which was of direct use, the problem of origin of organs may be within the reach of this law. The vertebrate eye, for example, is a marvel of adjustment and could never be explained by natural selection if it

had appeared originally as an adjusted series of parts. If such had been the case natural selection might have *preserved* but never *produced* the eye. This organ is, however, one of the best illustrations of the principle of natural selection, since it is one of the most intricate mechanisms. If it is possible to explain this organ without intelligent design and by the use of blind forces, it would seem possible to explain almost anything.

Now it happens that nature has left so many traces of the method which she adopted in building an eye that we can follow the history almost step by step. It is not in the vertebrates, indeed, where the process has been studied, but among the molluscs, where a very similar eye has been produced. The studies of the last fifteen years have shown us the steps in the formation of an eye and have shown them not as hypothetical, possible stages. We have actually found animals possessing eyes in the various stages of development. The history is something as follows:

The first step was simply the appearance of little pigment spots in the cells forming the surface of the body (Fig. 1). It is such a common thing for pigment to appear in superficial cells that it need not excite comment. These pigment cells were, however, connected with nerves, like other cells of the body, and when a number of such pigment cells chance to be near each other they form a first step in the formation of an eye. Such pigment will absorb light more than will the surrounding unpigmented cells, and this will produce an effect upon

FIG. 1.

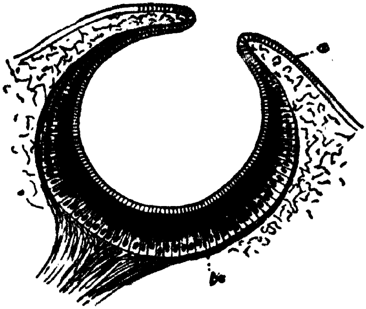

FIG. 3.

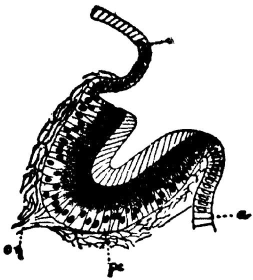

FIG. 2.

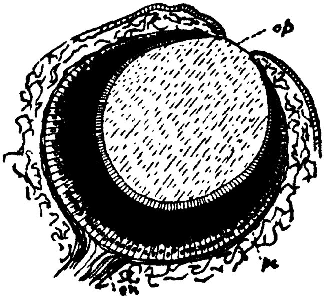

FIG. 4.

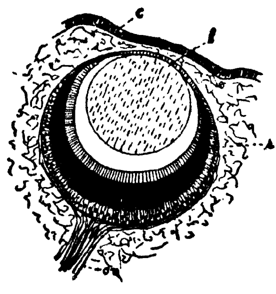

FIG. 5.

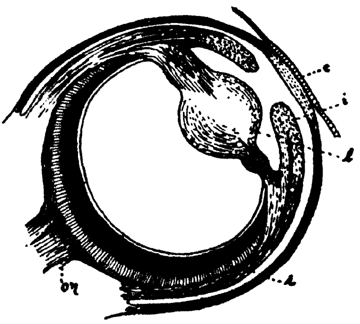

FIG. 6.

FIG. 1. A simple pigment spot: *a*, ordinary epithelial cells; *pc*, pigmented cells; *n*, nerve fibres. FIG. 2. Eye spot of Patella; *on*, optic nerve. FIG. 3. Camera eye without lens, the cavity filled with water. (Nautilus.) FIG. 4. A camera eye with a large lens filling its cavity. FIG. 5. Camera eye with cornea, *c*, covering the lens. (Murex.) FIG. 6. Complete eye with lens, *l*, cornea, *c*, and iris, *i*. (Cuttlefish.)

the ends of the nerves which are within these cells. Such a group of cells would thus be differently affected by light and darkness, and the animals possessing them would therefore be able to distinguish between light and darkness. Manifestly such a power would be of some use to its possessor and "would be seized upon by natural selection and fixed," by which expression is plainly only meant that animals possessing such pigment spots would in time replace those without them, this advantage being sufficient to enable them to be victors in the struggle for existence. As a fact, such simple eye spots are very common among animals.

But the more efficient the eye the more value would it possess. To be more efficient it would be necessary, first, that a larger number of pigmented cells should be grouped together. Manifestly if such cells are crowded together their efficiency will be greater than if they are scattered over the surface indiscriminately. If, therefore, amid the indefinite variations, there should appear some individuals with these pigmented cells raised on folds or sunken into pits (Fig. 2), these animals would have a greater concentration of the pigmented cells and they would thus have an advantage over animals where the cells were more scattered. These would again be preserved by natural selection and a second step in the formation of the eye would be taken (Fig. 2).

If such a pit should be partly closed at the mouth, as in Fig. 3, it is evident that a more efficient eye would be formed. The cavity would be

filled with water, since these animals are all aquatic, and such a small opening, by a well-known principle of optics, would tend to produce a faint image upon the sensitive surface within. We should have in fact in such an eye a " pin-hole camera " (Fig. 3). This organ would now actually be an eye, although still an imperfect one. It would have a decided advantage over the earlier types and would, therefore, be preserved by natural selection. Such eyes are actually found, Fig. 3 being a figure of the eye of a living animal. It would plainly be a still further advantage if these sensitive surfaces within the pit could be protected from external injury. This is accomplished in two ways. First, we notice that a thin film of skin grows over the opening, closing it completely. This skin, however, remains transparent, to allow light to pass through, and becomes a cornea (Fig. 5). Second, we find that there is secreted from the cells of the animal some transparent semi-liquid material to fill up the cavity, a necessity now, since water no longer enters it (Fig. 4).

The next step which we find is the formation of the transparent material in the eye cavity into a more solid body with curved surfaces (Fig. 5). This becomes a lens which will now focus the rays of light upon the sensitive surfaces lying behind it. Such an eye allows much more light to enter the eye and produces a sharper image than the pin-hole type, and it has, therefore, a very decided advantage. Its possessors would clearly be the ones to survive the struggle for existence, since clear sight would

be of very great advantage in the struggle for life. In the same way it is easy to understand that natural selection would preserve those individuals in which an opaque fold has partly grown over the lens so as to shut out the most oblique rays of light, which would otherwise confuse the image (Fig. 6). This curtain becomes an iris, and with this change the complex eye of the Squid (Fig. 6) is complete, only a few further changes in detail being needed to produce the highest types.

The significance of this illustration of the action of natural selection lies in two facts. 1. The stages referred to are not imaginary ones, but every one is actually found among existing animals. 2. Each new stage has given its possessor a decided advantage over the individuals with their eye in a lower stage of development, and hence each stage would come within the influence of natural selection. Each stage is a distinct advance over the last, and, therefore, granting that there have been sufficient variations in the pigment spots, skin foldings, etc., we can easily see how natural selection has actually taken the place of intelligent design in building the parts into a harmonious unity.

Such is the principle that Darwin offered to replace intelligent design. Given the five links in this chain and it is evident that species will be constantly undergoing changes. If the environment remained constant an equilibrium would soon appear. But the environment does not remain constant and with every change in the external conditions some new variation will render its possessors best fitted

to the struggle. Selection will then preserve the individuals with this new character and thus add the character in question to the inheritance of the race. Species will thus be built up, step by step, the principle of the *utility* of the accidental variations that arise being in all cases the guiding force which determines survival.

### *Facts to be Explained by Natural Selection*

In considering the significance of natural selection it is well at the outset to notice that there are three somewhat different problems to be solved in explaining the origin of species. They are *Adaptation, Divergence*, and *Discontinuity*.

*Adaptation*.—The first problem is the adaptation of structure to function, the origin of the mechanisms of which the organic world is so full. This above all things is the problem which natural selection aims to solve. It does this by showing how such structures have been built, step by step, each step, however, being a complete organ with a definite and useful function. If an adaptive organ were of no use until it was fully formed, with all its parts adjusted to each other, it would be impossible to explain its origin by natural selection of such minute variations as nature commonly offers the naturalist as data. The variations which we find are commonly small, being usually only slight departures from the character of the parent. Parents have an average length of wing, and the offspring will show wings in some cases slightly longer and

in others slightly shorter than this average. All variations will thus be centred around a mean represented by the previous generation. But natural selection shows just how such variations may be the origin of complicated organs. For example, in the formation of the eye it will be certain that the individuals which have reached the stage represented by Fig. 3 will show variations in regard to the size of the opening of the pit. Some will have an opening smaller and some larger than the mean size of the previous generation. But since the narrow opening would produce a sharper image the individuals with the opening smaller than the mean would be the ones to be preserved and hence the average size of the opening *among the survivors* would be smaller than the average size of the opening *among the individuals born.* The next generation would, of course, benefit by this, and thus natural selection, by simply picking out the best of these slight variations around the mean, will be able to produce a change in structure always in the direction of improvement. Clearly, then, to make the selection principle applicable, it is necessary to show that adaptive structures have been of slow growth and produced as the result of a series of steps, each of which is of distinct value. For this reason it is that students have been trying to show that complicated organs have thus been developed through the accumulation of little steps.

Were we to find evidence of the *sudden* appearance of a complicated organ, with its parts already adjusted to act in harmony, then, manifestly, natural

selection would utterly fail as an adequate explanation. But there is no evidence of such a phenomenon. On the contrary, evidence all goes to prove that all organs have been the result of slow growth. The study of nature has shown that animals were not created in their present form, but arose through a series of stages, each of which represented a complete animal. So, too, do we learn that each organ, however complicated it be at present, has slowly grown into its present form through a series of stages, each of which represents a complete organ with a definite use. In some cases it may be that the organs have not always been used for the same purpose in the different stages. The lungs of land animals have probably been derived from the air-bladders of fishes. The air-bladder of the fish is a much simpler organ than the lung, and could not be used for respiration. But we have little difficulty in discovering the several steps in the development of the lung from the air-bladder, and in each stage the organ was of use, although not always for the same purpose. In the fish it is a hydrostatic apparatus, and not until the fishes came out of the water did it become functional as a respiratory organ, although traces of this function are found among fishes that remain most of the time in the water. Thus it is everywhere. The study of anatomy, paleontology, and embryology has been wonderfully successful in tracing to their simple origin many of the complicated organs, until we may say that there is every reason for believing that adaptive structures have *always* developed by slow steps. The problem for

the evolutionist thus becomes simply the problem of explaining the origin and preservation of these various steps.

*Divergence.*—The study of animals and plants from every standpoint shows that the history of the origin of species has been one of divergence from common centres. The descendants of an animal have commonly not taken any one line but two or more, which have diverged from each other until several species have arisen. The explanation of descent must of course include this divergence. We can easily see how natural selection may modify descendants along some definite line, but why should these descendants take diverging lines of descent? Why should they not all be modified in the same direction if only the best fitted survive? This question of divergence is really a very fundamental one, for species have everywhere arisen in this manner. We shall see later that this problem has resulted in a very considerable modification of our understanding of the method of the action of the law of natural selection. At this point it will be sufficient to show by an illustration how such divergence may arise.

Imagine that at a certain period in the earth's history great fishes pursued smaller ones. The smaller fishes in their attempt to escape would swim into shallow water. When the tide fell some of them, with especially powerful muscles, would succeed in working off into deep water. Others, unable thus to escape, would be stranded on the sands, and would lie here till the tide rose again. Some

would, of course, die, but others might not die, for the reason that they chanced to have their air-bladder capable of acting as a slight respiratory organ, just as it does in some fishes to-day. These fishes would be kept alive by this slight respiration until the tide rose again. There would thus be preserved by natural selection *two* types, the one with strong muscles and the other with a well-developed air-bladder. Now let this process be repeated, and it is evident that the offspring of the original fishes would diverge from each other, the one group tending to become powerful swimmers and the other acquiring the power of using the air in respiration. The one would remain fishes while the other might form the starting-point of air-breathing animals. Natural selection thus preserved two types of "the fittest," and the result has been divergence. In this illustration, as we shall see later, there is involved a new principle of *isolation*, but at this point it will be sufficient as an illustration of the fact that natural selection may act in such a way as to produce divergence.

*Discontinuity.*—The theory of descent tells us that the history of living things has been a continuous one, every species having been connected with others by a continuous series of connecting links. This, however, is not the condition of life to-day. On the contrary, animals and plants are separated into hundreds of thousands of independent isolated groups. Allied species, although much alike, are not connected by intermediate links. It is true that such connecting links are sometimes found, but

when they are found they are regarded as matters of especial interest, a fact which in itself shows their rare occurrence. Certain it is that species are commonly separated by rather sharp lines of demarkation. In spite of continuity of descent, there is discontinuity of groups of descendants. Evidently the laws under which species have developed have been such as to have produced this discontinuity. The law of natural selection accounts for this more readily than it accounts for divergence. Natural selection is really a law of elimination rather than selection. The fittest survive only as the least fit perish. Hence the production of a new type presupposes the extinction of the older one. It will, of course, follow that intermediate forms will disappear as the extremes develop, the fact that a new type has arisen meaning that the older type has been distanced in the struggle for life; thus as lines of descent diverge, the connecting links between them will be exterminated by the struggle. From the very outset of the discussion of organic evolution there have been constant demands from the opponents of the theory that connecting links should be found. If descent has been continuous, where are the numerous indefinite connecting links which should have existed between the types which are isolated to-day? As we understand the law of natural selection to be one of elimination we see that this demand has no significance, for such connecting links have been exterminated by the very conditions which produced the new types.

### *Strength of the Law of Natural Selection*

There has certainly never been propounded any law connected with living phenomena which has received such general attention and excited so much discussion as this law of Darwin's. Ever since it was propounded in 1858, it has been subjected to criticisms which are even to-day nearly as strong as ever. The great weight of the theory is evident at once. In the first place the law may almost be regarded as a self-demonstrated truth. It is so clear that there is a struggle for existence, and so clear that in this struggle those best fitted for it will be the victors, that the survival of the fittest may be regarded as an axiom requiring no proof. Moreover, it is equally sure that animals and plants vary, and that the offspring tend to inherit the characters of their parents. The law of natural selection is thus much more intelligible than the law of gravitation. Gravitation is absolutely unexplained. We know the facts but not the causes. The law of natural selection is perfectly logical and easily understood. Given the conditions, and the results follow of necessity. It is true that we shall have to ask some questions as to these conditions, and to ask how efficient the law is in producing species, but the law itself is a logical conclusion and contains within itself its own proof. We may question the efficiency of the law in explaining the facts supposed to be reached by it, but we cannot question the law itself.

Again, the law finds strength in being so plainly ever active. The struggle for existence is constant.

It may be greater at times than at others, but it is always a force. All animals and plants are at all times in competition for sustenance, and at all times, therefore, this law of elimination crushes out of existence those least fitted to live. The constancy of its action makes the force a very efficient one.

Again, it is clear that this law not only accounts for gradual changes in type, but it explains, and indeed demands, a continual progression upward. In each generation it is the best that is preserved for breeding. If variations appear on each side of the mean represented by the parents, it will of course follow that the individuals will show variations in advance of their parents as well as variations of an inferior grade, and, since only the best are preserved, the survivors will tend to advance. Such has ever been the history of life. Beginning with low and simple types, there has ever been an advance. Animals have become larger, better equipped for offence and defence, better provided with organs for gaining food, better developed in every way as the ages have passed. Throughout the whole line there has been an ever-increasing tendency to a differentiation of labor among the different parts, which has always resulted in the organism being better served. Differentiation means higher structure, and, since variations toward a higher structure will commonly tend to make the individual more efficient in its struggle for existence, it will follow that natural selection will commonly be a force urging the line of development *upward*.

In the very opposite direction the theory has

equal strength. While it is true that in the vast majority of cases studied the best-developed individuals are the ones to be preserved, it is equally clear that under some conditions the reverse will occur. Natural selection will preserve the variation which is best adapted to the condition *in which the animal lives.* Now, while a high grade of structure will commonly render the individual better fitted for the struggle for life, there may be conditions in which a high grade of structure is actually a detriment. External ears are for most animals an advantage since they improve the hearing, but when a mammal acquires a habit of burrowing under the ground the presence of external ears would be manifestly a disadvantage, since they would be constantly receiving injury as the animal burrows through the soil. Natural selection would therefore here preserve individuals with least prominent ears and thus cause their disappearance, as it has done in the moles. Similar results arise when an animal acquires the habits of a parasite. To a parasite organs which were of use in a free life may become a positive disadvantage; locomotive organs, for example, injuring rather than benefiting. Here, then, natural selection will select individuals with less and less developed organs. Natural selection will thus explain *degradation* as well as advance in structure. In other words, while it is always the fittest that survives, the fittest is not always the best. That such degradation is frequently found in parasites is well known, and one of the strongest points in favor of the theory of natural selection is its ability

to explain such degradation of structure amid the general advance toward higher types.

Organisms are everywhere provided with organs for their own use. It is a matter of no little significance to find that an animal's organs are always for its own use and not for the use of other animals or plants. If there could be found any organism with a structure developed solely for the use of other animals or plants, the theory of natural selection would fail. But such instances are not found, and their absence is still another support for the theory which makes utility the basis of evolution.

But, after all, the greatest strength of the law of natural selection has been in the fact that it has furnished a natural law as a substitute for supernatural intelligence. In the making of worlds and the forming of mountains and valleys, blind force, as studied by the astronomer and geologist, appears to be sufficient, for here there is no adjustment of part to part for definite ends, such as characterizes machines. In the structure of the bodies of animals and plants the case is different. Natural force is blind and cannot be supposed to have any knowledge of the relation of parts adjusted for definite purposes. This seems to imply intelligence, and herein lies the difficulty in applying to living phenomena the same principles of natural law as have been successfully used to explain other natural phenomena. But natural selection seems to furnish a substitute for intelligence. It shows, in other words, how it may be assumed that even blind forces can be sufficient to adapt parts to each other

and construct the complicated organs which appear to be such indications of intelligence. Here, then, is the great secret of the influence of natural selection. It replaces a transcendental explanation by a natural one. To be sure, it does not explain force, and thus leaves the whole subject shrouded in as deep fundamental mysticism as ever. But science does not hope to explain force and power, and will be satisfied to account for natural phenomena by the action of natural forces acting in accordance with natural laws. Natural selection was a great step in this direction.

### *Development of the Doctrine of Natural Selection*

It can easily be understood that it required at least a quarter of a century before this theory of Darwin's could receive any calm discussion. It was received with violent opposition. The simple fact that it proposed to substitute natural for supernatural law was enough to arouse a very widespread disapproval. Not only was this opposition developed from the standpoint of theology and philosophy, but it was almost as strong among scientists. At first the theory was adopted by only a very few of the younger scientists, while the older men were cautious about accepting it, or even rejected it. The arguments against it were for years mostly *ad captandum* arguments, simply designed to demolish the theory rather than to discover whether or not it was true. Some twenty-five years were required in this preliminary sort of strife before it was

really possible to discuss the question calmly as merits a scientific theory. Even yet there is too large an amount of personal prejudice in the discussion of the theory to induce the most satisfactory results. Scientists are too sharply divided into followers and opponents of Darwin to promise the best results in determining the truth.

Of course the first necessity was to become accustomed to the idea of organic evolution. Natural selection, as propounded by Darwin, carried with it the whole doctrine of the descent of species from earlier species, involving, in short, the theory of organic evolution. Now, while this idea was not absolutely new to science, it was nevertheless new to most scientists and practically new to all other thinkers. It was a complete revolution of the mode of thinking, to abandon the earlier notion of distinct creation and substitute for it that of the origin of all species by simple descent. Naturally the first question to be widely discussed was the truth of the general theory of evolution, and until this matter was in a measure settled it was manifestly impossible that there should be any candid discussion of the doctrine of natural selection. To anyone who doubted the truth of organic evolution the theory of natural selection was sheer nonsense. As is well known, the opposition to the descent theory raged hotly for many years. Theology, philosophy, and science all disputed it, and during this time any rational judgment upon the theory of natural selection was impossible. Although during the twenty-five years following Darwin the subject

of natural selection was discussed, the real force of the discussion lay around the problem of the truth of the theory of descent. Personal prejudice rather than argument too often determined the results.

After a quarter of a century, however, the idea of descent became so familiar as to form a part of scientific belief, and then the *method* of descent could be more calmly discussed. Then there began a more careful study of the weak points in Darwin's theory, and, in the last fifteen years, the light which has been thrown upon the subject has given a much clearer conception of its significance. It should be possible to-day to discuss the value of the theory, uninfluenced by prejudice, and to reach a somewhat reliable opinion as to its force. The fact that Darwin accepted a doctrine should no longer be regarded as an argument either for or against it.

From the very first it has appeared that natural selection meets with many rather serious difficulties. Many of them were perceived by Darwin, and were carefully considered by him. In the later editions of his *Origin of Species* the most serious difficulties in the way of the acceptance of his theory were discussed. To most of them he found an answer which appeared satisfactory to him, but he acknowledged that the discussion of twenty years had convinced him that he had at first overrated the efficiency of the principle of natural selection. In his latest writings he still regarded this law as the most potent influence at work in the origin of species, but recognized that other agencies had been concerned to a greater extent than he had at first been inclined to

believe. It is important to remember this final attitude of Darwin in view of the rather surprising development of the belief in the efficiency of natural selection which has arisen since Darwin's death. As we shall see, there has arisen in later years a school of evolutionists that places natural selection upon a higher pinnacle than it was placed by Darwin.

In our consideration of the discussion of this law of Darwin, which is going on to-day as vigorously as at any time since it was promulgated, we ought to recognize at the very start the real question at issue. The question is not whether natural selection is a real factor in the production of species. This is acknowledged by all students of science. Indeed, it is hardly possible to conceive of anyone who really appreciates the meaning of the doctrine holding any other opinion than that it is a force of great weight. This is not a matter that needs longer any demonstration or discussion. The real question is not the efficiency but the *sufficiency* of the law. Natural selection is a factor in the method of descent. Is it the only factor? Will it explain all problems connected with the origin of species? In the sometimes bitter discussion of the last fifteen years it has been too frequently lost sight of that the real question is not the *efficiency* but the *sufficiency* of natural selection. That it is a force all acknowledge; that it is sufficient to account for all characters of species is quite another question. Our scientists are trying to discover the method of the origin of species, and the explanations which they offer must reach all kinds of characters. While we

cannot hope that every individual character of all species will ever be accounted for in detail we must at all events account for all classes of characters. In their admiration for Darwin, and influenced by certain lines of thought to be noticed later, some naturalists have concluded that natural selection meets all questions. The real problem which we must consider, therefore, is not the efficiency of this factor, but its ability to account for all classes of characters which have appeared during this process of organic evolution.

### *The Character of the Study which Natural Selection has Hitherto Received*

The study which this subject has received up to the present time has been largely theoretical. It has been by arguing as to what probably would occur under certain hypothetical conditions rather than by observations of what actually does occur under actual conditions. This is unfortunate, for it has been too frequently learned that theoretical deductions, unverified by experimental data, are very likely to be erroneous. But in this case the theoretical discussion has been a necessity. In the first place, the production of new types is admittedly a matter requiring a long period, and the short time which has been given to the study is yet too brief to offer direct results by observations. Moreover, the experimental method of study is debarred here from the very nature of the problem. The very essence of the law is that it acts under natural

conditions. The moment we introduce artificial conditions, that moment the result ceases to be one of natural selection. All kinds of experiments are based upon the production of artificial conditions, and this manifestly makes such experiments no tests of natural selection. Artificial experiments have been carried on for centuries by our horticulturalists and breeders, but they do not reach this question of the origin of species under nature. Thus the only means we have for getting evidence is by long continued observations under natural conditions. It is, of course, true that Darwin founded his theory originally upon observations. For many years he patiently collected data to verify his doctrine before it was propounded to the world, and it was for this reason that the theory was from the first so firmly established. But after Darwin, for a quarter of a century little advance was made in the actual study of natural selection in nature.

Most of Darwin's evidence was obtained from the study of animals and plants under domestication. While it is true that such evidence gives most valuable data for the study of variation and heredity, it can only in an indirect manner bear upon the problem of natural selection. Artificial breeding may show what great variations may be possible among the descendants of an animal, and how such variations may be selected and preserved. All such facts are of course of the greatest significance in the study of the method of the origin of species, but they give no direct evidence of the method which was followed in nature. Recognizing, then, that it may

perhaps require centuries for the production of new species, how is it possible to get any direct evidence of such processes by observation? It is because of this difficulty that the study of the problem has been hitherto largely theoretical. The only methods of reaching the proof seem to be indirect. We must study animals under domestication and learn as many facts concerning inheritance and variation as possible. We must study animals and plants under nature, and find out how closely the conditions agree with those under domestication. We may then draw our conclusion from such facts as to nature's method of producing species. It may be long before we can hope to find any direct instances in nature of the actual production under our eyes of new types.

Nevertheless, as we shall see in a later chapter, in recent years there has begun a more logical attempt to test by observation these problems of selection under nature. The work involved is enormous, since it means the collection and most accurate study of thousands of specimens. As our naturalists are now looking upon nature they find that occasionally we have offered to our inspection some experiment carried out by nature on a grand scale. We have, for example, quite a number of instances where plants or animals are introduced into new countries in which their environment is entirely changed. Such instances offer excellent opportunities for the study of selection. These examples are only just beginning to be made use of, but the lessons from them are already of significance, and will

be referred to in later pages. In general it may here be stated that these observations, few as they are, do show that natural selection is a force which is, with more or less constancy, eliminating the unfit. A fierce winter storm in New England, for example, plays great havoc with the imported English sparrows. A comparison of animals that die during such a storm with others that recover from its effects shows that certain types of birds are being eliminated. The survivors are those with small bodies well supported upon strong legs, while those that die are larger but with weaker legs. This elimination will leave only the birds best fitted for the climate, and is, of course, an instance of natural selection. Such observations are as yet very few, but as our naturalists more clearly perceive the problems which confront them we may hope that a more extended study of the actual working of natural selection in nature will take the place of the study of phenomena under domestication.

### *Summary*

Having accepted the conclusion that species have been derived from earlier ones by descent, the question of the laws that have produced this origin of new species, the *method* of descent, comes to the front. The method must clearly be something which will replace the intelligence which controls the making of an artificial machine. It must plainly be based upon the factors of variation and reproduction, since these are the two great points wherein a

living machine differs from an artificial machine. Darwin brought evolution into prominence because he suggested such a method. This was based upon the fact that animals and plants always tend to vary, and that variations may be accumulated in successive generations, as is shown by artificial breeding. As a substitute for the selective power of the breeder he offered natural selection. This was simply the fact that in the intense struggle for life, to which animals and plants are subjected, only the best of these variations will succeed in producing offspring. Successive generations will accumulate such favorable variations, causing a gradual perfection of parts and a constant change of species. This theory offers utility as a principle which guides the course of descent. It is applicable therefore only to such characters as are of use, and only to such as have been built by an accumulation of slight variations. This law is offered as the explanation of adaptation, divergence, and discontinuity, the three chief factors to be accounted for in explaining the origin of species.

Natural selection soon found active support from scientists because it offered a natural explanation for what had hitherto been regarded as supernatural phenomena. It appealed to science as a self-evident truth, as ever active, as accounting for a general progress of organisms as well as for the origin of new types, and explained equally well the occasional degradation of type under certain conditions. The law was at once the battle-ground for debate, which has been for a quarter of a century

mostly of a theoretical character. This debate has been largely influenced by the personal prejudices of the disputants, and this personal dispute lasted until the general idea of evolution became familiar. Then calmer judgment was possible, and a discussion of more value as to the real cogency of the law of natural selection became possible. Having finally clearly recognized that the doctrine of the evolution of species does not depend upon the acceptance of natural selection as a sufficient cause, naturalists have been able to view this great law of Darwin's in a clearer light.

# CHAPTER III

## DISCUSSION OF DARWIN'S LINKS—PRODIGALITY, STRUGGLE, SURVIVAL

THE evolutionary problems in the last two decades have centred around the theory of natural selection. There are, of course, many other questions that have demanded wide attention, but most of them can, after all, be regarded as outcomes of the doctrine of Darwin. Darwin saw the problems of nature very clearly, and he had the genius to present them in a comprehensive theory that has served as the basis of investigation for nearly half a century. For this reason, in order to understand the present attitude of science toward the method of evolution we must base our discussion upon this theory.

As we have seen, natural selection is a chain of five links, and the more we study natural phenomena the more comprehensive do these five links appear. Prodigality, struggle, variation, survival, and heredity certainly include nearly all phases of living phenomena which can be studied with the hope of reaching the solution of the descent problem. The

secret of organic evolution must be concealed among them. In our study of the Method of Evolution we can therefore do no better than to take up first these five links in order and learn what has been added to or subtracted from each during the forty years that have passed since Darwin bound them together as a connected whole. Two of them we shall find remaining practically as he understood them, while the other three have had a flood of light thrown upon them. While there has been no great change in the conceptions of prodigality and struggle, the other three links of the chain would to-day hardly be recognized as the same factors with which Darwin was concerned when he first made his attempt to explain the origin of species.

### *Prodigality in Nature*

The fact that all animals and plants tend to increase by normal processes of reproduction faster than is consistent with support has only become more and more manifest as the years have passed. Nature seems to have endowed most species with an extraordinary and seemingly unnecessary power of multiplication. We have learned of animals and plants that can multiply with a rapidity even greater than any which Darwin mentioned. A species of tape worm (*Echinococcus*) is said to be capable of producing in a single generation a number of offspring represented by the figures 150,000,000,000, a number simply beyond human comprehension. Certain bacteria multiply so rapidly that the descendants

of a single individual, if allowed to multiply unhindered for three days, would be represented by the figures 47,000,000,000,000. While these are extremes, an overwhelming prodigality of reproduction appears everywhere. No animal or plant has been found that does not have powers of multiplication which surpass the possibilities of sustenance.

It may seem a little strange that nature should be thus prodigal, for we do not commonly expect to find such wastefulness. In general, in the growth of animals and plants both, nature seems to be quite parsimonious. Organs which are not used are quickly reduced in size even to disappearance. Living things do not, as a rule, develop characters for which they have no use. It is true, as we shall see later, that there are apparently some useless characters among animals and plants; but they are connected with organs of small size, and require no special expenditure of energy to sustain or produce them. But with this reproductive power the reverse seems to be true. The possibilities of reproduction are far beyond the needs of the species. If there is room for only two individuals it seems a waste to produce a hundred. Moreover, the production of these numerous individuals is not, like the general development of useless organs, a matter which requires the expenditure of only a little food and energy, and hence of little significance to the adult. On the other hand, the production of young is the one great object of the life of the animal and plant, and frequently the life of the individual is sacrificed in the production of the numerous offspring which

it leaves behind. Many an animal uses up all its energy in the reproductive act, even the magnificent salmon frequently sacrificing its life in ascending rivers for the sole purpose of depositing its eggs. There must be some reason for this prodigality here amid a general parsimony. Why should nature be so prodigal even to the extent of sacrificing life?

It is not difficult to answer this question provided we accept the law of natural selection. It is this prodigality alone that makes natural selection a possibility; this alone that has made organic evolution a possibility, since it is by the selection of the best among the great numbers that the gradual elevation of type has been brought about. But, since the statement just made involves purpose, which the scientist seldom recognizes, a more strict statement would be as follows: Only such animals and plants as have developed this excessive power of reproduction would be subject to selection, since these alone would be engaged in a struggle for existence. Advancement in structure is only possible where natural selection eliminates the unfit. Hence it is only among animals that multiply rapidly that there can be a development due to the preservation of the best varieties. There may have been many animals and plants in the history of the world without this excessive power of multiplication, but they have been inevitably exterminated. Even if they were able to maintain their life for a time they could not advance, since advancement comes only from the elimination of the unfit. As a result, individuals with lesser fertility would soon be distanced in the

struggle for life by those that were advancing by selection. Hence we can readily understand how this prodigality of nature has been brought about, simply from the fact that all types of organisms which did not show it could not advance into higher grades of structure, and were therefore soon exterminated.

If this prodigality of nature is the basis of natural selection there ought to be exceptionally good chances for the action of the law among those groups of animals where the prodigality is the greatest. It is interesting to note in this connection that, among higher animals, it is in the insects that we find the greatest powers of multiplication. It is said that three flies can consume the carcass of an ox quicker than a lion can. The flies deposit their eggs; the eggs hatch in five or six days; the larvæ feed upon the flesh and soon become adult and deposit eggs in their turn. Larvæ and adults together would consume the flesh in an incredibly short time. Insects have an extraordinary power of reproduction, held in check by a lack of food. Now it is among insects that we find some of the most remarkable examples of adaptation. Mimicry, an example of which has been mentioned, is certainly one of the most extraordinary facts in nature, and this mimicry has all its best examples among insects. It is among insects, too, that instincts are best developed. Now in the development of instincts we find one of the most difficult problems for natural selectionists to meet, and it is certainly suggestive to find their highest development among

animals where the prodigality is especially well developed. Where the number of individuals is the greatest the elimination will be most severe, and hence the chance for the preservation of favorable variations will be greatest.

It is unnecessary to dwell longer upon this topic. The prodigality of nature is a fact of universal occurrence, and the studies since Darwin have all increased rather than diminished the importance which he placed upon this factor in nature.

### *Struggle for Existence*

The struggle for existence follows from the prodigality of nature, but it is difficult or impossible for us to realize the intensity of this struggle. To the superficial observer nature appears peaceful enough, and to one who watches the flowers in bloom and hears the birds sing, it seems incredible that this seeming peacefulness should conceal a condition of absolutely universal warfare of extermination going on all the time under our eyes. But such is certainly the case, and all who have had an opportunity of studying animals and plants in nature have been impressed with this ever-present struggle. We have learned more of the manifold phases of the struggle year by year. From the very moment that the egg is produced by the mother it is subjected to a host of influences tending to destroy it. As the days and months pass while the egg is developing to the mature animal these hostile influences are multiplying, the number of individuals

becomes less and less, and finally only a few survive all dangers and are able to reproduce their kind. These individuals are the ones who have stood all the tests and are capable of living because in the thousands of tests they have universally come off victorious. Of course the struggle is not always equally severe. There are periods of rapid extermination, like a severe winter storm, followed by periods of comparative ease. But every individual that reaches the reproducing age must be looked upon as the successful competitor of a long series of examinations.

*Man.*—The completeness with which this idea of struggle has become a part of our knowledge is indicated by the fact that the term struggle for existence has passed from its original significance and has become a part of common language. One hears constantly of the struggle for existence, and as frequently used the term refers to the struggle of man for bread. Now the struggle for existence as understood by the scientist and as forming part of the general theory of natural selection, is a very different thing from the struggle for existence as the term is used in its application to mankind. Unfortunately, this difference is not always recognized, and questions concerning the evolution of man are often confused by the improper use of this principle. The social struggle of man for bread has practically no relation to the struggle for existence, which lies at the basis of natural selection as a factor in the evolution of animals. It is necessary to perceive this difference, or our logic will be fallacious.

The struggle for existence which forms the basis of natural selection is actually a struggle for life, in *which the unsuccessful individuals are eventually exterminated.* If it is a struggle for food, it is not simply a struggle to see which shall get the best food, but a struggle to see which shall starve. The result is life or death, or, more correctly, offspring or no offspring. The struggle for existence among men is, however, very different. Men do indeed struggle for food, but it is really to see which shall have the best food or get it most easily, and not to see which shall starve. Actual starvation among civilized men is a phenomenon so rare that it does not enter into the problem of human evolution, at least in its present condition among the higher races. Unless the struggle is such as to lessen the reproductive power of the defeated individuals, it is not a struggle for existence at all in the sense in which it is used by biological science. Every poverty-stricken individual who survives long enough to leave offspring is a victor in the struggle as understood by science, while he who inherits his millions but leaves no children absolutely fails, even though his life is one of the greatest apparent success.

Now there are, it is true, severe struggles among men for sustenance, struggles so severe as to make man's life a burden. But in the scientific sense nearly all men are victors. Some are obliged to work very hard while others acquire their sustenance with comparatively little labor. But all obtain food enough to keep them alive, and, so far as reproduction is concerned, it is well known that the most

hard pressed in the struggle, *i. e.*, the poor, are commonly the ones who produce the largest number of offspring. The severe competition for bread which is found among the lower classes, or the struggle for wealth and social position among the higher classes, has no relation with the struggle for existence which lies at the basis of the law of natural selection. There are writers who have compared with the struggle for existence the competition of men in business, in politics, in social aspirations, the competition for money, and, in short, all kinds of human competition. Nothing could be more illogical. The victors produce no more offspring than those less favored, and usually not so many. Unless the struggle is such as to touch the matter of life and death, or at least the ability to leave offspring, it is not a struggle for existence in any way comparable to that found among animals, and which serves as the basis of an evolution of type.

There are two quite distinct phases of the struggle for existence. One is a competition of animal with animal, and the other the struggle against adverse physical conditions. The former comes chiefly when more individuals are born than can find sustenance, or when strong enemies become abundant. If an animal have territory enough and food enough its struggle for existence is chiefly with other organisms that try to capture it for food. Now mankind is practically exempt from either of these types of struggle. He occupies a territory that he does not yet by any means completely fill. In his early

history his condition was doubtless different. Living upon fruits which he gathered, and upon the flesh of animals which he could capture, early man had no great food supply, and actual competition must have been more severe. Warfare, as we know, was then constant, and this warfare meant struggle to the death. But after man learned to cultivate the soil and raise cattle for food, the whole problem changed. These new habits greatly enlarged his world. Even yet he has by no means increased to the limit of the world's sustenance. Except for occasional famines there always has been, and still is, more than a sufficiency of food for all men that are born, and, so long as this continues, mankind can have no conception of what is meant by the struggle for existence among animals. When mankind multiplies until the world is filled and he is using each year all food that can possibly be produced by the cultivation of the land, then, and not till then, will begin his experience in the struggle for existence as it occurs among the lower orders of nature to-day.

Mankind, by his intelligence, has also made himself superior to the second phase of the struggle. He has mastered all animals, and, with certain exceptions to be noted presently, needs fear no competition with them. He is equally superior to physical conditions of nature. The cold or heat, the storm and the drouth, hardly influence him, and are not for him factors in the struggle for existence. While such influences occasionally may produce the death of a few individuals, the effect is so slight as to be

inappreciable in the general history of man. In all of these lines, where the struggle for existence is so ruthless in eliminating unfit types of lower animals and plants, mankind is exempt. He is superior to all this sort of struggle.

But mankind is not exempt from an actual struggle for existence. Although no more are born than can find sustenance, and although he is constantly increasing in numbers, a fact which indicates that the struggle for existence is not severe with him, still it is certain that more are born than succeed in reaching maturity. If we ask what agencies prevent so many from reaching maturity and producing offspring, we shall see wherein lies the actual struggle for existence among men. Actual battles in warfare take away some and accidents remove others. But the real contest that mankind is engaged in is twofold. His most serious contest is with parasitic foes. Microscopic organisms, producing as they do various infectious diseases, are man's most serious enemies, and the most efficient agencies in preventing many individuals from producing offspring. With them he has a struggle from the very beginning of his life. His second conflict is with alcoholism and sensualism. These two factors are constantly working among men, and seizing and eliminating the weak. No family lasts long after it becomes a victim to undue alcoholism or sensuality. With these hostile forces mankind is in vigorous conflict, and his struggle for existence is pressing. But nothing is more certain than that the competition among men for a livelihood, the contest for wealth and

power, the competition in business, have no connection with the struggle for existence, and any theories based upon a supposed similarity of such a "struggle for existence" as it occurs among civilized man and the struggle for existence among the lower orders of nature is fallacious at its very foundation.

*Lower Animals and Plants.*—Whatever be said of this struggle for existence among men it is severe enough among animals and plants, and many have been the facts collected to testify to the fact. Perhaps the most striking testimony is found in instances where, for certain exceptional reasons, the struggle is temporarily checked. There are many good illustrations of this phenomenon. For example, between 1850 and 1870, about 1500 English sparrows were brought into the United States. In England these birds are not especially abundant, a somewhat constant small number remaining year after year. In England they have various enemies, animate and inanimate, to contend with, and these are sufficient to keep them in check. Their struggle for existence is a severe one, and a comparatively few of those born succeed in reaching maturity. But it was impossible to appreciate the severity of this struggle until the birds were removed from it. When introduced into America all their ordinary enemies disappeared. In the new country there was food in plenty for them, and the many influences which had curbed their reproductive powers in England were removed. As a result a larger number of individuals reached maturity, and they

began to increase with extraordinary rapidity. Now they are found in great numbers, while their relatives in England still remain as a small species with comparatively few individuals. This shows that in their own home there is a severe struggle for existence that keeps down the numbers.

The Colorado potato beetle may serve as another example. This is a beetle that formerly fed upon certain wild plants in our western States. It was not especially abundant, since its food was limited and the struggle for existence held the species in check. But when man began to cultivate the potato in the region the beetle began to feed upon this new food plant. Its food supply was thus very suddenly increased, and this was the same as if its struggle for existence had been checked. There was no longer a question as to which of the larvæ born should obtain food, for there was enough for all. The result of this cessation of the struggle for existence was to allow the reproductive powers free play, and for a few years the species increased with prodigious rapidity until it now extends over most of the United States.

Such instances might be multiplied indefinitely, for they are very numerous. To get the full significance of the struggle for existence it is only necessary to compare the condition of the English sparrow in England with its condition in America, or to compare the potato beetle before and after the cultivation of the potato in the western States. Such a comparison will give a faint idea of what this struggle really means.

Among plants the struggle is no less severe, although it takes a different form. Here there is, of course, no question of actual contest of individuals with each other, but the passive struggle for food or for a place to grow is just as severe as among animals. The rapid distribution of European plants introduced into America is an illustration of the cessation of the struggle among plants comparable to those mentioned among animals.

It must not be supposed that all the study given to the subject has enabled us to explain in all cases the details of this struggle for existence, or even to tell in what it consists. We cannot tell, for example, just what forces are at work in England to check the expansion of the sparrow, and which are withdrawn when the birds come to America. We cannot say why it is that the so-called white daisy (*Leucanthemum*) finds its foes among American plants so much more easy to overcome than its foes in Europe. We cannot tell wherein the struggle for existence which the rabbit experiences in England is so much more severe than that which it finds in Australia. We cannot tell why some orchids are so rare and the dandelion so common, since either of them is capable of multiplying rapidly enough to fill the world in a few years. But the facts known in regard to the rate of multiplication and the numerous examples of the results which follow the removal of the restrictions to the multiplication, show plainly enough the extraordinary influence of this struggle for existence.

All animals thus have a fecundity capable of filling

the world with offspring in a short time, but in all cases this fecundity is held in check by various conditions. Every animal is struggling to reproduce as fast as possible, but the struggle with conditions holds all in check. Remove the check and the animals increase prodigiously until they meet a second check which curbs them once more. Reproduction, being by geometrical ratio, is a force whose power is almost infinite. The struggle for existence is the curb which holds it in check.

It is evident that in this point lies one of the reasons why the study of animals under domestication must fail to give us any notion of evolution under nature. In domestication the reproductive powers are checked by many artificial conditions. There can be no struggle for existence among them. The only struggle, or semblance to a struggle, is that found in the endeavor, unconscious, of course, to please the fancy of the breeder, since those that please him are preserved and the others sacrificed.

### *Struggle for the Life of Others*

There is a reverse to the struggle for existence which has been made much of in recent years by some authors. This is the principle that leads organisms to undergo hardship, suffering, and even death for the benefit of other individuals. Among animals below man it is seen chiefly in the sacrifice of the mother for the good of the offspring. As already noticed, it frequently happens that the mother uses up all her energy in the reproductive

act. Among higher animals, mother-love influences the action of animals to a certain extent and for brief periods. Among social animals it frequently happens that the individual has instincts which compel it to sacrifice itself for the good of the social group of which it is a member. Among social insects the soldier ant does not hesitate an instant to sacrifice its life for the colony.

This principle is, of course, in a sense the reverse of the struggle for existence, in which each animal is endeavoring to sustain its own life. It may be expressed as a *struggle for the life of the species* rather than the individual. Among the lower animals and plants it is really indistinguishable from the struggle for existence as we have outlined it, for, since a struggle for food is a struggle for power to grow, and since growth is followed by division, the struggle for the life of the species and the individual are identical. Among higher animals, where mother-love or social instinct lead to actual sacrifice, this second principle of sacrifice, or *altruism*, as it is called, undoubtedly plays an important part. It is, however, chiefly in man that the force comes into active prominence. Among animals it is only with the higher groups that it is of much significance. It is therefore a law that must be chiefly studied later in connection with the evolution of man.

### *Survival of the Fittest, or Natural Selection*

For the purpose of clearness in our discussion we will take up the subject of survival before that of

variation. The survival of the fittest is, of course, the keynote of the whole theory — is, in short, natural selection. According to the accuracy of this conception the whole theory stands or falls. But this problem of survival stands to-day in quite a different light from what it did when first advanced by Darwin. The term survival of the fittest, like that of struggle for existence, has become a familiar phrase, and in a similar manner is frequently applied to matters affecting social problems leading to very fallacious conclusions. This, however, need not detain us. The weight of the law of the survival of the fittest has come largely from the study of the breeding of domestic animals; for it is the study of animals under domestication which has furnished hitherto the largest part of the evidence for the descent theory. It is a well known fact that the breeder is able to mould the bodies of animals almost at will. By simply turning his attention to some particular point in structure and then selecting and mating together animals showing peculiarities in regard to the point in question, he is able to get offspring in which the desired character is, on an average, more highly developed than the average of the previous generation. By again selecting the individuals which show the character best developed, and mating them together, he is able to advance the next generation still farther. By a continuation of the process of selection his breed in time undergoes great change. The differences in the breeds of pigeons, horses, grapes, and roses are illustrations of the possibilities in this direction. These are facts,

not theories, and show what great changes are possible, within the limits of a few generations, by the action of the simple forces of reproduction and heredity, provided there is present some *selective force* to guide the process. Of course, if left to breed at will, these animals would never have mated together as the breeder mates them, and no such accumulative results would have been obtained. But the facts of domestic breeding show that it is only necessary that the process should be properly guided in order to produce profound modification upon the structure of the animals, modifications sufficient to produce radically new types.

These effects have been commonly produced by the process of *selection*, not by direct modification. The principle of selection is coming to be recognized as one of very wide-reaching influence. It reaches far beyond the breeding of animals. It permeates all life. It is a factor in civilized society. It is by selection that individuals are set apart for higher positions or higher advantages. Selection pushes our children on in their education or holds them back. By selection, the psychologist tells us, the child learns to walk, simply selecting the useful from among the numerous indefinite purposeless motions which he makes with his legs at his first attempt to use them. By selection, too, mental habits are formed. Indeed, throughout organic life the principle of selection is a prominent force. Of these numerous types of selection we are here concerned with only one.

## *Natural Selection*

When we consider what the breeder can do by selection we see that if some natural force could be found which could take the place of this selective power of the breeder, we should have the problem of the method of the origin of species largely solved. This force Darwin found in the fact that, amid the constant struggle for life, only those animals would survive that were best adapted to their conditions of life, and hence it would follow that the best adapted individuals must always mate together, since these alone would survive to maturity. For the artificial mating together of varieties at the caprice of the breeder, is substituted the principle of *utility*, which mates together only such animals as show the highest variations in the direction of utility. Having thus discovered a force which replaces the fancy of the breeder, it is easy to claim that this force, natural selection, may be expected to do anything that a breeder can do in the way of moulding species. Indeed, it is said that it may be expected to do more, for while the breeder's selection is fitful, natural selection is always active. Utility is a constant force, artificial selection a spasmodic force, and much more may be expected of the former than the latter.

With this statement we come right to the centre of one of the most serious objections to natural selection, an objection so serious as to have led some scientists to abandon natural selection as a sufficient cause. In the discussion of this principle

of survival there has been too frequently a jugglery of terms somewhat as follows: Animals best fitted to their conditions will survive. The best-fitted animals are those with useful variations, and hence natural selection seizes useful variations and preserves them. Therefore *any* useful character may be preserved. The logical position, that all animals which survive possess useful characters, is made to mean that *all* useful characters will be picked out by natural selection. Hence it has been assumed that it is only necessary to show that a character is of some use, no matter how trivial, and it is proved that the character has been produced by natural selection.

Now this interpretation is manifestly an illogical one. It certainly does not follow from the premises, and if it is true it needs further explanation. Natural selection is not a force like that of the breeder who looks over his animals and selects some few that have a given character especially developed. The word " selection " is here misleading. There is in nature no selector and no selecting. Nature does not select the best, but simply eliminates the worst. There is a great difference between a process that consciously picks out the best and one that unconsciously eliminates the worst. With the latter process it is necessary, in order that any particular character be preserved, that it should not only be of *some* use, but should be of sufficient utility to control at some period the matter of life or death, or at least the production of offspring. It cannot be preserved by natural selection un-

less in time all animals that are in direct competition, but without the character in question, are exterminated. Its possession must be of sufficient value to determine that its possessors remain while other non-favored individuals succumb to the struggle for existence. A character is not simply preserved because it is useful, but because it enables its possessor to win in the struggle where others without the character in question would fail. This is a very different statement from that which says that natural selection will preserve all useful characters. It would seem very questionable whether all characters which are of some slight utility to their possessor could be of sufficient use to the individual to control the matter of his life or death. But unless this occur, unless the character in question bring it about that the favored alone leave offspring while the unfavored ones leave, at least, a smaller number and thus eventually become exterminated, clearly the principle of survival can have nothing to do with the preservation of the character in question. To be preserved by natural selection a character must be of "*selective value*," which means that it is sufficient to protect the life of its possessor at the expense of individuals not possessing it.

In considering the force of this fundamental question we must first ask how rigid is the action of this principle of survival. Is the struggle for existence of such a character that only the least fit are exterminated, and that therefore the best fitted *always* survive? No one will pretend that this is the case.

The conditions of life are too complicated to make such a rigid selection possible. The problem of the survivor will in many cases depend upon accident, entirely independent of fitness. Many eggs of fishes which float freely in the water are devoured by other animals, and devoured indiscriminately, no question of fitness coming into the problem at all. A whale swimming into a school of small molluscs opens his huge mouth and takes in hundreds of individuals indiscriminately, no question of fitness affecting the survival of the remainder, but only the accident of happening to be out of the reach of the huge mouth. This indiscriminate destruction occurs constantly, and certainly influences the problem of survival. Of the hundreds of individuals that are produced where few can live, many are destroyed indiscriminately, independent of the principle of survival of the fittest, and of these that are thus killed doubtless some are superior to those that survive. This principle of indiscriminate elimination does not in the slightest deny the force of the principle of survival of the fittest, but only indicates that its action is not absolutely rigid. The fittest do not always survive, for many of them are destroyed.

On the other hand, the least fit do not always perish. Whether an individual shall live or die in the struggle is largely a matter of accident. Many a well-equipped individual will die, while many another, even though handicapped by decidedly unfavorable characters, will continue to live and produce offspring because of some specially favorable

conditions. Nothing could seem to be more decidedly disadvantageous than a broken leg, and, if the principle of elimination of the unfit were rigid, broken-legged individuals should be speedily destroyed. But it is quite common to find animals with broken legs or arms which yet succeed in living perfectly well. They have repaired their broken members by processes of bone growth, and have been able to carry on their part in the struggle for life and survive competition. I have found a frog with the whole of both feet bitten off, and yet with the wounds healed, the animal living without feet, and hence hardly able to swim, but side by side in competition with other well-developed animals. I have found a clam that in its young condition had received a severe rent in one gill, through which, by some twist the body had been thrust, giving rise to the extraordinary condition of three gills on one side of the body and one on the other, a truly monstrous abnormity. But this clam had lived to maturity, and produced eggs in quantities equal to any other clam.

Now such instances simply show the complexity of the conditions which determine survival. They indicate that these animals were favored in some respects sufficiently to counteract the disadvantage of their mutilations. But the fact that so many instances are found does show that single characters do not always determine survival or elimination. The question whether an individual survive is dependent upon many factors, of which utility of various organs may be one and accident another.

What would seem more sure from a logical standpoint, than that, in the intense struggle for life due to numerous individuals seeking for food, a frog who was unable to swim because of the loss of his feet would be sure to be a loser? Even if the inflammation caused by the wound did not destroy him, it would seem impossible for the animal to obtain his share of food. Of course, a footless race would be eliminated in a comparatively short time, but the survival of so many mutilated individuals shows that selection is not so rigid as to eliminate *all* unfit individuals, even though their disadvantage be very great.

If a very disadvantageous character may thus fail to produce destruction it must be still more true that a favorable character, occurring in a single individual, has really little chance for survival. The individual possessing it will have to compete with accident, with indiscriminate slaughter, and with other conditions which we have just seen may be sufficient to preserve even a broken-legged individual. Nothing can seem more evident than that the web of the foot and the muscles of the legs are of use in swimming, and have therefore been developed by the preserving influence of natural selection. If anything is of selective value, these characters certainly are. But when we find that a frog with *no feet* can survive the struggle for existence, it is evidently difficult to believe that single variations, either of use or disadvantage, will have any special likelihood of surviving at the expense of other members of the race, so as eventually to replace all

others. But only thus can they be "seized upon by natural selection and preserved."

### *Selection Based upon Mean Types*

These facts, together with others to be noticed later, force us to the conclusion that this principle of survival must act upon general averages rather than upon individual variations. This conclusion is one of the most important modifications of the selection theory which has been made since Darwin. Independent of such great peculiarities as broken legs, etc., the individuals of a species will be found to show variations above and below the average. If we pick out any character we shall find that the animals of the species will, in reference to it, be grouped around a mean. For example, if we measure the length of the beak of sparrows we find some birds with long and others with short beaks. It is evident that in this respect, roughly speaking, about half the birds will have beaks above and half below the average length. Now, if it be an advantage for the birds to have longer beaks, it will follow that there will be a tendency for the shorter-beaked birds to be eliminated in the struggle. While any individual short-beaked bird may be favored by conditions and survive, there will in general be more short-beaked birds destroyed than long-beaked. The average length of the beaks of the *survivors* will thus be greater than the average length of *those born*. Suppose, for illustration, the length of the beak be represented by numbers, then the relation

of seven birds to this law might be expressed by the following figures:

| | | | |
|---|---|---|---|
| Length of beak of seven individuals before elimination.......... | 3 | Length of beak of survivors after elimination. The birds represented by the blanks are supposed to have been destroyed............ | – |
| | 4 | | – |
| | 5 | | 5 |
| | 6 | | – |
| | 7 | | 7 |
| | 8 | | 8 |
| | 9 | | – |
| | 42 | | 20 |
| Average of all birds.... | 6 | Average of survivors.. | $6\frac{2}{3}$ |

If thus the average length of beak of the survivors is greater than the average of all birds born, it logically follows that the next generation would tend to inherit a beak whose average is greater than that of the last generation. Of course the greater the number of individuals taken into account and the more severe the elimination, the more certain will it be that the mean length of the beak of the survivors will be greater than that of the individuals born, provided, of course, that the greater length is actually of advantage.

We can thus see that survival might affect general averages more readily than individual variations. If the conditions should remain constant, variations from the mean would soon cease to accumulate. The race would rapidly reach a point where departures either above or below the average would be unfavorable. When this occurred survival would tend to retain the average individual, and, while there might be slight fluctuations around this point, the mean would remain practically unchanged. But conditions never do remain constant. With changes in climate, in movements of the earth's surface, in

migrations of animals and plants, the environment is always undergoing change, and, with the change of conditions, it will, of course, follow that the average character which is best adapted to the conditions of this year may not be adapted for the conditions of next year. If this occur, the mean character will tend to move, and the race will change once more by the selection of the best average individuals. A change in conditions will thus greatly affect the question of what individuals would survive. The survival average will be a constantly varying one. A new set of conditions might make those individuals fittest for the struggle that departed farthest from the mean. Thus, as environment changes the type will change, and only so long as conditions remain constant will the type remain without change. But *if the environment should remain constant the type may remain unchanged indefinitely*, as has been the case with some types of animals that live under exceptionally unvarying conditions, and have remained unchanged from early geological periods. Some types would be expected to change slowly and others rapidly. But in all cases it will be by the survival of averages rather than individual characters. Individual variations count for little; variations above or below an average count for much. The race develops by masses rather than from individual freaks.

*Utility*

The essence of the principle of the survival of the fittest is utility. Artificial selection is replaced by

the survival of the majority of such animals as have the most useful peculiarities. This principle is well calculated to account for the origin of adaptations. The fact that different organs are so well adapted to their purposes that they are like delicate machines with parts adjusted to each other, has been the great mystery of living phenomena which seemed to demand some explanation outside of natural forces. The principle of the survival of the fittest seems to meet the demand by showing how these adaptations have been produced by slow growth, successive useful steps being preserved generation after generation and added to the whole. The problem of the origin of adaptations has been the great study since Darwin pointed out the method. We can now readily see how this principle may furnish an explanation of all useful characters, granting for a moment the appearance of useful variations to be selected.

But how is it with characters that have no utility? It is, of course, a great achievement to be able to point out the method by which adaptations have been produced, but if animals have some characters that are *not* useful, natural selection does not explain them. Natural selection can develop useful organs only. The real problem which our naturalists are trying to solve is not the origin of *adaptations* simply but the origin of *species* also. Now while many of the characters and organs of animals and plants are of utility to the individual there are others that appear to be useless. As animals and plants are studied, it is found that the different

species differ from each other by certain definite characters. These distinctive peculiarities that distinguish species are called "*specific characters*," and this term will be hereafter used in this sense. The explanation of the origin of species must then account for the origin of specific characters. Now specific characters are frequently trivial in nature. This was long ago recognized by Darwin, who saw that the characters by which species are distinguished are frequently so trivial as to be apparently useless. If, however, we are to explain the origin of species we must find an explanation of these trivial characters as well as the more important ones. If these trivial characters are of *no* use to their possessors, then manifestly the principle of the survival of the fittest does not account for them. The fact that species are so commonly separated by characters that seem to be absolutely useless has led some of our keenest naturalists to insist that the survival of the fittest does not explain the origin of species, but explains only the origin of adaptations. At all events, it is clear that the problem of the utility of specific characters is a very fundamental one to the discussion of the principle of survival.

We here come to the first parting of the ways between scientists of different schools. On the one hand we find those who are so thoroughly convinced of the universality of the principle of natural selection that they insist that all specific characters are useful, however useless they may seem. It is beyond question that they are led to this belief in the utility of all characters, not from observation, but

simply from their belief in the sufficiency of the law of natural selection. They tell us that we know too little of the actual life of organisms in nature to enable us to say that any given character is not of use; and to make a claim that anything, no matter how trivial, is useless, is simply to confess ignorance. We must acknowledge that many seemingly useless organs have been found to have utility as soon as the life habits of animals are better understood. Certainly, utility has been found more universal than was believed to be possible a quarter of a century ago. The followers of Darwin have given very much attention to this matter. They have pointed out many lines of utility hitherto not dreamed of. They have considered great multitudes of cases of seemingly useless characters, and by a little imagination have suggested some use to which they may be adapted. If one reads the recent works of Wallace, the most prominent advocate of this position, he will not fail to be impressed with the fact that utility is much more widely applicable as an explanation of seemingly trivial characters than might have been thought possible. The position held by this writer is, that inasmuch as the law of natural selection is a universal force which all admit, while all other forces of evolution are yet in dispute, and inasmuch as so many seemingly useless organs have been shown to be of use, it is perfectly legitimate to claim that when we come to understand them, we shall find that all characters are of value, and that the principle of survival of the fittest has been concerned in the development of them all. If this

is true, the survival of the fittest explains the origin of species as well as the origin of adaptations, since *all* specific characters are really adaptations.

But on the other hand, many naturalists think that there are specific characters for which we can not only see no utility, but which are demonstrably of no use. A few illustrations will serve to make the matter clearer. Certain insects are distinguished from each other in accordance with whether they possess one or two bristles on the head. Here is a character which appears to be constant, and which must therefore be explained by any complete theory of the origin of species. Can we imagine that the question of whether the animal has one or two hairs should ever have been of selective value? But if developed by natural selection, this character must at some time have been a matter of life and death. Again, among snails, the shells commonly coil in the same direction in the same species, this fact making the direction of the coiling of the shell a specific character. But clearly this is not a matter of selective value, since living among the rest of the individuals will frequently be found some with their shells coiled in the opposite direction. Again, horses have small horny callosities on their feet. No one has suggested any possible use for them, but nevertheless they are present on the feet of all the species of the horse family. But the most curious fact is, that while the horse has them on all four feet, the ass has them on only two. Now, upon the principle that utility is universal, it would be necessary to claim, not only that the presence of

four callosities has been a matter of selective value in the horse, an extremely difficult thing to believe, but also that the presence of only two instead of four has been of selective value in the ass. This position approaches absurdity. Again, there are molluscs characterized by special markings of the shell, which markings are constant enough to be specific characters, and must, of course, be included in any explanation of the origin of species. But these marks are demonstrably of no use, since they are entirely covered by the epidermis of the animal when alive, and absolutely invisible. Again, some birds have slight differences in color markings which separate species. Now these differences may perhaps be regarded as of use as protective or as recognition marks. But in some cases the color markings are entirely concealed by other feathers and, being invisible, can be of no possible utility. It is hardly possible for one, unless he has decided previously to accept the all-sufficiency of natural selection, to believe that there can be any utility in the very slight differences in the shapes of the leaves of plants, in the microscopic markings of the hairs of different species of mammals, the exact numbers of the feathers in the tails of birds, the peculiar distribution of the veins in the wing of a butterfly, the microscopic marking in the scales on its wings, or a host of other similar trivial characters. When it is remembered that the selection principle would force us to insist that all these characters are of value sufficient to protect their possessors at the expense of other individuals not possessing them,

it is evident that the burden thrown upon the principle of survival becomes very great. When finally we come to characters of specific nature connected with color markings which are invisible when the animal is alive, there is apparently no resource left except to conclude that the principle of survival because of utility does not account for everything.

### *What is Meant by "Selective Value"*

How useful must a character be to be of selective value? Such a question it is of course impossible to answer. The preservation of any particular character is not an isolated matter. It is not single characters that are preserved, but a combination of many characters together. The survivor is the animal showing the best combination of characters. It may even have some harmful ones, provided the useful ones predominate. The rattle of the rattlesnake has at times doubtless been of a disadvantage to its possessor, and has caused the death of hundreds of thousands of individuals. It is doubtless possible to show, as Darwin did, that it has also been of value to the animals. But how are we to decide whether its use or disadvantage is the greater, except by the theoretical conclusion that it must on the whole be useful or it would have been eliminated? The whole study of utility is sure to result in an unsatisfactory circular logic something as follows: The survival of the fittest is a law. If an organ be not useful it could not have been developed by natural selection. Therefore all organs and all

characters must be useful. Since in such a problem no one can prove a negative, this position cannot be disproved, but it is certainly not very satisfactory.

But with all this criticism of utility it must be recognized that the agency of utility as determining survival is becoming more significant as discussion proceeds. We have seen that it must be admitted that all characters to be affected by the principle of survival must have selective value, *i. e.*, must affect the matter of life and death. But this demand does not prove to be so serious when we recognize that natural selection works upon general averages rather than individuals. Those who find the selection principle such a great factor insist that all characters have selective value if they have ***any value at all.*** If a character has the value of even rendering its possessor a little more comfortable, they tell us it will eventually be subject to the principle of survival at the expense of non-favored animals. The substitution of old types by new ones is not a matter of a single generation but many generations. In such a long history there must be innumerable conditions where any character, even the slightest, may have been of use enough to give its possessors an advantage over others. It is not necessary to believe that a character should preserve its possessor, while *all* non-favored individuals perish, in order to consider that the character has selective value. Considering that the origin of species is a matter extending over hundreds of years and many generations, even little things will count in the long run. If an animal has a slight advantage over another

which simply gives it more comfort and enables it to obtain its food with a little less exertion, this may tell permanently in the struggle, since such an individual will have more energy to put into reproduction, and hence may leave a larger number of offspring. The other non-favored individuals may not indeed be exterminated without offspring, but may simply produce less offspring. In this struggle for permanency the individuals which have the largest number of offspring, other things being equal, will inevitably come out ahead, and the others in time disappear.

An example will make this clearer. A difference of an inch or two in the length of a cow's tail seems a matter decidedly too small to base the selection principle upon. Can it be imagined that the lengthening of the tail by a couple of inches can be of selective value? Can we honestly believe that these two inches will determine that the longer-tailed cow will live and produce offspring while the shorter-tailed individuals will die? Only thus, however, can we assume that the tail has been developed by natural selection. Now this example, which seems to be an extreme case of slight utility, may show us how it is possible, upon the principle of the selection of averages, to conceive that characters of slight use *may* be preserved by natural selection. It is not necessary to suppose that the long-tailed individuals are preserved by this extra couple of inches at the expense of the shorter-tailed individuals in order that the character may be within the reach of natural selection. If the animals are

troubled by insect pests, it is certainly a matter of convenience to them to have a tail long enough to brush off the flies, and the longer tail, within certain limits, will be more useful than a shorter one. It is not likely that this will preserve the life of a single individual, but it will follow that the animals with longer tails will be less irritated by insects than those with shorter tails. Now, although this would not affect the matter of life and death, a nervous irritation would pretty surely interfere with the reproductive efficiency. An animal that is constantly bothered by insects will have less nervous energy to devote to reproduction, and therefore such a constantly irritated animal would be likely to be somewhat less prolific than one less irritated. From this it would follow that the half of the animals with tails a little longer than the average would be pretty sure to leave a somewhat larger number of offspring than the half whose tails were below the average. But a slightly increased fertility of this sort would, in the course of a few generations, see the long-tailed animals becoming more and more numerous, until they would eventually replace the others.

Thus it is claimed that any character which is of even the slightest value will, in the long run, have its influence upon the race and be preserved by the principle of the survival of the fittest. Animals and plants are constantly upon the defensive against a host of adverse influences, and the battle only ends with death. Indeed the battle does not end with death, but is taken up by the next generation, and, although there may be variations in its severity,

the struggle never ceases. In this long contest anything that will make the animal more comfortable will give it more vigor and be a deciding factor in determining productiveness. The demand that a character, to be of selective value, shall be of use enough to preserve its possessor while others die is misleading. If the advantage is sufficient to enable one animal to obtain its food with a little more ease, or to escape from its enemies with a little less exertion, or be less irritated in the struggle for life, it will enable the individual to produce a larger number of offspring, and these offspring, inheriting the characters of their parents, will for the same reason produce a larger number of offspring in their turn. Numbers will tell; and in the course of time the descendants of the individuals with the slightly increased reproductive powers will supplant the less-productive individuals, and in this way a character, of even the slightest utility, may be preserved by the survival of the fittest. In the long run animals with such slightly useful characters will be the survivors even though these be insufficient to determine that the non-favored individuals shall die. The extinction of lines of descent is going on much more constantly than we think. Even among men, where the struggle for existence is least, statistics show that families are constantly dying out. It is of course impossible to determine exactly what factors bring about the extermination of so many families, but the fact is plain to anyone who will look around him, and the study of the genealogy of small communities shows that it is really a comparatively small

number of lines of descent that succeed in perpetuating themselves indefinitely. Now if this is true among men where the struggle is least, much more true must it be among animals where the struggle is so much more severe; and if lines of descent are being constantly blotted out, it is clear that slight factors may be determining causes.

But after all, this extending of the contest over many generations does not affect the conclusion that the value of any character must be in its influence upon the individual at some definite time. If the character in question is to be preserved by survival, it must be of vital importance to the *individual*, or it has no influence upon the race. It is sometimes stated that natural selection is directed toward the species and not the individual, the individual being ruthlessly sacrificed for the benefit of the species. Doubtless this is true if the good of the individual is in opposition to the good of the species. In some cases an organism uses its entire energies in the reproductive process, and dies immediately after. Here the individual is clearly sacrificed to the species. But this sacrifice occurs only at the end of an active life, and the individual must survive the struggle for existence until the reproductive period arrives. In this earlier life natural selection must be directed toward preserving the individual even though now he is to be sacrificed. Among the higher animals, moreover, the reproductive period is extended over a long time, and here the individuals that live the longest will produce the most offspring, and be the most likely to per-

petuate their race. The principle of survival would thus preserve the offspring of the longest-lived individuals. Extending the struggle over many generations does not therefore change the fact that the useful character, in order to be preserved, must act to preserve the individual or to increase the number of offspring. If, therefore, the shorter-tailed cow produces less offspring than her longer-tailed sister, it must be either because she does not live so long or because she fails to produce offspring in some seasons. We are, therefore, still forced to claim that of the addition of the extra inch or two in the length the tail has at some time, either decided the matter of life and death, or has determined whether or not a calf shall be born and reared. To put the matter in other words, we must say that if the mean length of the tail were two feet six inches, those individuals with tails two feet seven inches long would have such an advantage over those with tails two feet five inches long that the former would leave more offspring. This must mean either that they live longer or are more fertile during their life. If it is a fact that they live longer, then we are forced to say that the possession of the shorter tail has really caused the death of the less-favored individuals. If it means a greater fertility, we must conclude that the extra inch of the tail has produced an increased number of offspring. Either of these positions is somewhat difficult to accept.

Upon this subject of utility there is thus still a difference of opinion. One side argues that any advantage, however slight, even if it simply gives its

possessor a little more comfort and ease, will in the end be seized by natural selection. The other side claims that it is too much for our credulity to require us to believe that an extremely slight advantage can become a matter of survival at the expense of other non-favored individuals, even though we extend the contest over hundreds of generations. Animals without these slight advantages can obtain food and leave offspring and it is a mere assumption that they leave fewer offspring. The principle of the survival of the fittest, as the explanation of characters, demands that at some time in the history of the race the possession of the character has been of *sufficient value to have caused the survival of the line of descent of animals possessing it and the final extermination of the line of descent of animals not possessing it.* The probabilities against such a result in the case of many characters of doubtful utility appear very great.

It is probably a fair statement to make, however, that the more this matter of survival is studied the more it appears that minute characters may play a part in the process. The struggle is at times so severe that the question of life or death may hang on a thread. Under ordinary conditions these little things may not count, but when times of stress come everything tells in the result. No one would have imagined that the survival of sparrows in a severe winter storm would be determined by such factors as minute differences in the length of wing, leg, etc.—differences amounting only to a very slight fraction of an inch. But such is found to be the

case. The progress of observation, in other words, quite decidedly weakens the force of the demand that all characters must have selective value in order that they be preserved by natural selection. It has rather tended to show, though not with complete satisfaction, that any character of value may be at times of selective value and if so may be preserved by natural selection.

### *Correlation*

The conclusion remains without question that all characters which are to be preserved by the survival of the fittest must be useful. Natural selection can only be directed toward utility and, in spite of the consideration mentioned in the last paragraph, there are many characters among animals and plants that seem to be absolutely useless. As one means of avoiding the difficulty arising here, emphasis has been laid upon what is called *correlation*. As organisms are studied it becomes more and more manifest that the whole organism is tied together in such a way that a modification of one part involves a modification of another. A single character rarely varies alone but is commonly associated with other variations. Variation in the hair usually means variation in the teeth. Increased numbers of tail feathers in pigeons are associated with increased numbers of caudal vertebræ. Increased size of feet in these birds commonly involves increased beaks. White dogs are subject to distemper and white fowls to "gapes." These illustrations show what is meant

by correlated variations. We can rarely see any connection between the different characters which thus seem to vary together. No one can suggest why the beak and the toes should increase in size together, but the existence of such correlations is positive.

Now by the skilful use of this principle of correlation many of the difficulties arising in connection with the problem of utility may be made to disappear. If a certain character which is manifestly of no utility be found in an animal, and we are unable to explain it on the ground of utility, it is only necessary to say that it is correlated with some other character which *is* useful and the difficulty disappears. If some birds have concealed colors which are distinctive characters of the species, we cannot indeed call them useful, but we may say that these colored feathers are correlated with other colors in visible feathers, and that the correlation is such that when the visible colors appear these invisible feathers acquire color also. The visible colors, however, may protect the bird from destruction and hence, as they are preserved by natural selection, the invisible colors will be retained also. These are preserved, not by their own utility, but because of the utility of the other peculiarity with which they are associated.

Of course if we use this principle freely to explain characters which appear of no use, we may remove all difficulties centring around the matter of utility. But the method is very unsatisfactory. Undoubtedly the whole organism is thus tied into a whole in

such intimate relations that one part cannot be modified without affecting other parts, but we know little or nothing in regard to this obscure topic. It is hardly satisfactory to explain one obscure subject by the use of another equally or more obscure. If actual study can show us some definite laws connected with this matter, if observation can tell us what kind of characters are inextricably bound together, if by the study of variation we can find out where it is legitimate and where illegitimate to apply this principle, then we may find in correlation an aid to the solution of the problem. No one will question that such a correlation does exist, and that when we understand it better we shall find it throwing light upon many a dark point. But it is entirely inadequate to fall back upon this solution of all difficulties which the problem of utility meets. Before correlation can be relied upon to aid much in the solution of the difficulty, it will be necessary to know something more about it than the vague idea that such a law exists. It will be necessary to know from observation something about variations and their correlations and such a knowledge hardly exists to-day.

### *The Problem of Variation*

Survival explains nothing unless accompanied by something more positive. Natural selection cannot act until there is something to select. The fittest cannot survive until the fittest appears. As one writer puts it, the fact that weak boilers explode does n't explain the existence of strong boilers. Until

some favorable variation has arisen it manifestly cannot be preserved by survival. Clearly the problem of the origin of variations and their nature is prior to the question of their survival. Survival may account for the preservation of animals which show favorable variations, and it may explain the accumulation of these variations generation after generation until complex structures are built, provided that the proper favorable variations appear. But the survival of the fittest does not in the slightest degree account for the origin of variations. The demand for something to explain the *origin* of variations is thus prior to the question of their *survival*.

The weight of this demand for something prior to the law of survival as the real explanation of evolution has appealed to different scientists with different force. In the minds of some it has been looked upon as such a forcible demand that it vitiates the whole doctrine of the survival of the fittest, and makes it no *cause* of the origin of species at all. Survival, they say, produces nothing; it only eliminates the poorest specimens that are produced by some more fundamental forces. It may have influence in determining the course of evolution, but it explains the origin of nothing. These scientists tell us that the real problem is not the *survival* but the *origin* of the fittest, and until we find out the laws under which new variations appear we have not advanced much, if any, toward the question of the origin of species. The force of this position is manifest.

On the other hand, to other scientists this criticism

appears to have very little weight. They point out that variations of all kinds do occur. These variations are not adaptive and have no reference to any particular purpose; the term diversity is better than variation to express their nature. They are indefinite, occurring in every direction. They are such variations which, as already noticed, present departures above and below the average. They are "hap-hazard," "fortuitous," and no more demand any special explanation than does the shape of a stone we may pick up. If we go into a quarry and pick up a chip of stone we have no doubt that the shape of the fragment is explained by the action of special forces which broke to pieces a larger stone of which this is a fragment. Its shape is undoubtedly due to definite laws, but so far as concerns any purposes for which we wish to use the stone, the shape is purely accidental, and no one thinks it necessary to demand an explanation of such irregular bits of stones. Thus may we look upon organic variations. They are fortuitous, and while each doubtless has its definite causes they are purely accidental so far as any purpose is concerned. Such miscellaneous variations do not demand an explanation any more than does the shape of the fragment of stone. Animals are sure to be unlike their parents. The legs of the child are bound to be a little longer or a little shorter than those of its parent. Now the theory of natural selection shows us how the simple survival of such accidental variations directs the course of evolution in definite channels. The real cause of the evolution is thus the law which determines the

survival of the varieties and not the forces which produce these accidental variations.. If we should find a wall built of rough natural stones, some big and some little, we should, of course, say that the force that built the wall was the man who selected these stones and put them into place, and not the forces of nature that broke the original bed rock into those particular fragments.

This illustration may be carried a little farther and will illustrate the difference between the two methods of viewing natural selection. If we should go into a quarry and find there a stone that was a perfect cube or a perfect sphere or had some other quite definite shape, we should at once ask for the cause of this peculiar shape. Blind forces of nature produce irregular shapes and not cubes or spheres. If we should find thus many stones of definite shape and shaped so as to fit into some plan, we should conclude at once that they were fashioned by some forces other than the blind forces of nature. If they are subsequently built into a monument, there is just as much need for explaining how the stones acquired their definite shapes, as there is to explain how they were put together to form the monument. In the same way if we find variations among organisms occurring in definite directions and plainly adapted to a distinct purpose, then here, too, we would be forced to ask for some explanation other than that of "hap-hazard." If they are irregular, indefinite, and occurring in any and all directions, then they would be like the chance stones picked up in the quarry; but if they are in

definite directions then they would be comparable to the fashioned stones designed for the monument. Here, then, is the real ground for the difference of opinion as to the value of the law of the survival of the fittest as an explanation of evoultion. On the one hand it is said that variations are constantly occurring on all sides and in all directions. Each doubtless has its cause but they have no relation to the purposes to which they are subsequently put by natural selection. They are hap-hazard and the survival of these hap-hazard variations determines the line of evolution. Survival is the real force which explains the origin of species, just as the builder who selects miscellaneous rough stones is the real force in building a wall. On the other hand, it is said that the variations are not simply fortuitous, that similar variations occur in many individuals at once, that they occur in definite directions and perhaps have some relation to the purpose to which they are subsequently adapted. If this be the case, they are like the fashioned building stones in the quarry, and the first problem in explaining evolution must be to account for these variations, their survival being secondary.

Which of these two views expresses the facts of nature ? Evidently this question must be answered by a study of variation. But before doing this it will be well to summarize the facts relating to the selection theory up to this point.

### *Summary*

**The problem of evolution must evidently be solved**

by the study of the five links that Darwin built into a theory, since they comprise nearly all of the phenomena of life. These five links have been given much study in the last quarter of a century. The first, prodigality in reproduction, remains just as it was conceived by Darwin. The second link, struggle for existence, has been brought into ever clearer light as the years have passed. The intensity of that struggle has been more forcibly brought to our attention by the extraordinary results which occur when it is temporarily checked, and we realize its constancy more fully to-day than at any time past. But this subject is so far misunderstood that the term struggle for existence is applied to mankind with a meaning entirely different from its scientific meaning. Mankind, as we have seen, has not yet encroached upon the limits of existence, and until that time comes he cannot experience the struggle of existence which is the lot of the lower animals. His struggle is chiefly with his microscopic foes, and the wide use of the phrase struggle for existence in reference to man's competition with man for the good things of life, is thoroughly unscientific and has led to very erroneous conclusions.

The force of the third link in the chain, survival of the fittest, is derived from the known effect of selection among domestic animals. By artificial selection the breeder is able to produce profound changes in the animals or plants with which he experiments. If a selective force of a similar nature could be found in nature the modification of species might be understood. This selective force is found

in the fact that the individuals with the most useful characters will survive, *i. e.*, will be selected to be the ancestors of subsequent generations. It has appeared, however, that this law does not select the best but simply rejects the worst. In order, therefore, that any character shall be selected by this principle it must give its possessor an advantage which will either preserve its life at crises when unfavored individuals will perish, or it must enable its possessor to leave more offspring and thus eventually exterminate its non-favored competitors. It must be of selective value. In asking what is meant by selective value we have learned, first, that this selection is not always rigid, and that even animals with very favorable variations will be frequently exterminated by indiscriminate destruction. We have been forced to the conclusion that single variations can rarely count and that evolution advances by averages and means rather than by individual characters. We have learned, however, that a character need not be of very great use in order that it may come within the reach of this law, provided it be such as can vary around a mean. Under these conditions it may enable its possessor to produce more offspring if it simply gives greater comfort. But on the other hand, it has appeared that there are many characters which seem to be absolutely useless and some that are demonstrably so. Such characters cannot be explained upon the principle of natural selection except by calling in the obscure law of correlation. Upon the question of utility, therefore, there is still found a difference of opinion. Some

*insist that all* characters are useful because they must have been produced by natural selection, and others claim that they are not produced by natural selection since they are not useful.

Lastly, we have seen that selection cannot act until there are variations to select from. If these variations are simply hap-hazard then we may look upon natural selection as the guiding force of evolution. But if they are in definite directions, or are adapted at the outset to the purpose for which they are used, then the primal force in evolution is something that has produced these variations. We, therefore, turn next to the study of variations.

# CHAPTER IV

## VARIATION

IF animals and plants produced their kind without variation evolution would, of course, be impossible. Variations are the stones out of which is erected the structure which we call the animal and the plant, adapted so marvellously to its conditions. It is highly important to know where these stones came from, and whether they were already shaped to fit the building before they were fixed by selection, or whether they were simply rough stones of indefinite shape, the shape thus appearing in the structure only as the stones were put in place. According to the first idea, variations are said to be *determinate*, since the direction of the variations appears to be determined by some underlying law. If such is the case, the real factor in evolution is not the survival factor but that which determines the character of the variations. If, however, the variations are purely hap-hazard, then the determining factor in evolution is the force that selects the variations which are to survive and become transmitted to future generations. In other

words, the difference in view which is most fundamental is whether the directive force lies in something which produces the variations or only in the law which preserves them. It is quite necessary to recognize this difference of view in order to understand how some scientists can hold that natural selection is a sufficient cause for the origin of species, while others hold that it is no cause at all. The whole question lies in the problem of variation. On the one hand, it is claimed that the selection of indefinite minute variations is sufficient to account for evolution; on the other, that it is necessary to find some other more fundamental force which can explain why these variations appear along special lines where they are needed.

There are three fundamental problems to be solved in the study of variation: (1) The nature of variations; (2) Are variations determinate or haphazard? (3) The origin or cause of variations.

Darwin studied this subject of variation very systematically, but after his *Animals and Plants under Domestication* it was some thirty years before a second serious attempt was made to investigate this important topic. In recent years an entirely new aspect has been given to the subject by the change of views that has been brought about by the theories of Weismann, to be referred to in the next chapter. The two subjects of variation and heredity are so intimately connected with each other that it is hardly possible to separate them. Evidently unless a variation is transmitted to posterity by heredity it can have no permanent influence upon

evolution. This subject must be considered in the next chapter, the present one being devoted to some of the general problems of variation independent of the matter of heredity.

### *Nature of Variations—Abundance*

That variations occur in abundance is palpable on every hand. To Darwin is certainly due the credit of turning attention to the fact that the organism is plastic. Before he had pointed out the significance of variations, the attention of naturalists had been given to the subject of adherence to type rather than to departures from it. As long as naturalists were hunting for species the subject of variation was largely ignored, but as soon as the importance of variations from the normal was recognized, discoveries followed rapidly. Darwin and his immediate followers, as was natural, studied variations among domestic animals and plants. Much more is known about domestic animals than wild ones, since they have been for a long time under careful observation. Since the breeders have always desired to obtain the best types, they have naturally noticed all little differences among individuals. Darwin found for this reason a perfect wealth of data already at hand in regard to variations among domestic animals. Moreover, it has been believed that domestic animals vary more than species in nature. This would not be surprising, since they are placed under very unnatural conditions, and if the environment has any influence in producing variations, as

has always been assumed, then it would be expected that animals and plants would show wider variations when cultivated than would similar forms living in nature and, therefore, presumably under more constant conditions. The variations which have been found among domestic animals are very great, and certainly offer to the evolutionist all the data he needs to build up a theory of evolution.

But, manifestly, variations under domestication, while very significant in their general bearing, must be of secondary importance to variations under nature. Darwinism has been frequently criticised because it is founded upon artificial rather than natural conditions. The evolution of species which science is trying to explain has occurred, not under domestication, but under nature. Although the artificial conditions of domestication may have produced great variations among animals, this fact gives no real data for explaining the origin of species. Variations among organisms living in nature must be relied upon for data to explain the evolutionary process.

Darwin had comparatively little information upon this subject. To determine anything in regard to it involves the collection and most painstaking study of thousands of specimens of the same species of animals, including careful measurements and comparison of parts. Such a study is very laborious, and had hardly been attempted even when Darwin published the last edition of his work. Within more recent years, however, data in these directions have been accumulating. Not a few

naturalists have undertaken the task of making accurate measurements of different parts of animals in large numbers of individuals of the same species, the comparison of individuals as to colors and markings, as to shapes of different organs, and indeed in all respects where data in regard to variation may be determined by measurement or comparison. They have tried to determine some facts in regard to the extent of variations, their abundance, their relations to each other, as to whether they are always of slight extent or whether they are sometimes very great, whether they occur in a majority of animals of a species or only a few, the rest adhering closely to the type, etc. In short, all questions which suggest themselves in this connection have been asked. The information now in our possession is very much greater than that upon which Darwin founded his theories, and it has already taught us to modify our conclusions quite materially in some respects.

Perhaps the most important lesson to be derived from the facts is that variation among animals and plants in nature, instead of being exceptional, is the rule. The more the matter is studied the more extensive do the variations appear. It even becomes a question whether animals and plants under domestication are more variable than animals and plants under nature. So impressed have some of our naturalists become with this fact that they are beginning to tell us that we have hitherto taken a wrong attitude toward the problem of species. They are telling us that a tendency to change is the most fundamental property of living matter; that it

is the ability to change that most clearly distinguishes living from non-living matter, and that this tendency is absolutely constant. So uniform is this property that the really difficult problem in evolution is, not to explain the production of variations, but to give some reasons why forms ever remain constant. Variability and inconstancy are the rule, stability the exception.

Now, while such views are somewhat different from the commonly accepted conception of nature, the very fact of their existence testifies to the growing belief in variation. Certainly, variability among species in nature is much more universal than even Darwin was inclined to believe. It must be admitted that most scientists have been a little surprised at this result. While variations have been expected by all, their abundance has hardly been anticipated. It has been generally supposed that adherence to type with considerable closeness is the rule, and the occurrence on all sides of such multitudinous variations as have appeared from the study of recent years has been unexpected.

These variations are of great variety and affect all classes of organisms. Naturally they have been most studied among higher animals which most attract attention, and as yet comparatively little is known in regard to variations among lower animals and plants. This may be due in part to the fact that the lower animals have not so many parts to vary, but it is chiefly due to a lack of careful observations. The lower types of animals are almost wholly aquatic, and manifestly it is much more difficult

to make extended observations upon them than upon land types. At the same time, even among lower animals, variations are found to be abundant enough when looked for. For example, our commonest species of shore snail varies very widely in size and shape. Gulick has found no less than 252 quite distinct varieties of a certain species of land snail. Insects show variability in marked degree, although their small size makes it impossible to discern variations which, if of equal extent in higher animals, would be very noticeable. Among larger animals variations occur in the greatest profusion. For practical reasons the subject has been most thoroughly studied among birds, where the general interest in the animals has caused them to be collected in large numbers. Among them there is not a single part of the body that does not show wide variations. They vary in the length of the bill, the length of the head, the toes, the wings, and the legs. They vary in the weight of the body, and in the weight as compared to the length of the legs and wings. They vary in color of feathers, even birds which seem very similar showing slight differences. The size, shape, and color of the eggs are widely different in individuals of the same species. In short, in regard to the study of birds where observations have been most carefully made, there is not a single part of the body that is measurable, and therefore subject to exact tabulation, that is not widely variable. Other features that are not measurable are more difficult to tabulate, such as differences in habit, in general shape of body, in strength,

etc. These, although not easily expressed by figures, are none the less striking to naturalists who have studied variation. Of course it is not to be expected that a very great amount of data will be obtained except among those animals that have been collected in large numbers. Little information could be expected from such animals as lions, bears, or larger mammals. At most, a naturalist might have half a dozen specimens to compare, and this number would be wholly insufficient to give any information of value. But so much information has been collected upon the subject in the last twenty years that it can be stated without danger of contradiction that, wherever animals and plants are studied in sufficient numbers to give reliable data, variations are found with a frequency that is surprising, and leads to the conclusion that variability or diversity is the rule, constancy the exception, if, indeed, such a thing as constancy is ever found. Apparently all animals and plants depart in some degree from the normal mean which the type is supposed to represent.

It is found further, that the amount of the variation is greater than had been at first supposed. Leaving out of account special cases called "sports," which must be considered later, it is found that among the individuals which would be called normal, the extent of the variation is frequently surprisingly great. When we find that among normal individuals the length of the tail varies twenty-one per cent., and the length of wing twenty-three per cent., it is clear that we are dealing with variations

which cannot be regarded as minute. As already noticed, one of the objections urged against natural selection is the difficulty of believing that minute variations could ever be of selective value. It was a weakness of Darwinism that it based selection so largely upon minute variations. But plainly a variation of nearly one fourth in the length of the tail is not a minute one and, if the tail is of any value so that variations in its length may be of use, a variation of twenty-three per cent., should certainly be enough to bring it within the reach of the principle of the survival of the fittest. Of course such variations are extreme and ordinary individuals do not show such wide differences, but their existence certainly suffices to show that natural selection has variations of considerable extent to act upon.

## *Variations Around a Mean*

If any organ be examined in a large number of individuals it is found to vary in such a way as to be better or less developed than the average. Taking any organ and comparing many individuals there is found a mean size for the species. Now when measurements are made it will be found that some individuals will have the organ larger and others smaller than the mean. In regard to any character all individuals of a species may thus be divided into two groups, one with the character more and the other with it less developed than the mean. Some few would doubtless adhere exactly to the normal average, but actual observation shows

that there is no very great massing of individuals around the mean. In other words while there are doubtless more individuals somewhat closely approximating the mean than at the extremes, still the numbers that depart widely from the average are very numerous. Variations of considerable magnitude are thus abundant.

Now if variations occur at all they must, of course, occur around a mean. We could expect nothing else, and the matter would not be worth mentioning were it not for its extremely important relation to the principle of natural selection as mentioned in the last chapter. One of the most serious difficulties raised against the theory of natural selection from the very beginning is the evident swamping effects of cross-breeding. It was early pointed out that rarely could a favorable peculiarity perpetuate itself. Even if it should be that selection could preserve an animal with some highly useful variation, this animal would be forced to breed with other individuals not thus favored, and the offspring would be expected to show the character in less degree than the first parent, since crossing with unfavored individuals would reduce rather than increase it. In the next generation, still supposing that the individuals would be obliged to breed with others not thus favored, the character would be still further reduced, and in a few generations would practically disappear. This fact of the disappearance of favorable characters by cross-breeding has always been recognized as a very serious obstacle to natural selection, and at one time Darwin himself

regarded it as so serious as almost to overthrow his theory. The result of the criticism has been practically to force us to deny that single variations can count for anything in the evolution of species. A variation appearing in a single individual will in most cases be eliminated by cross-breeding and only such variations can have much influence upon the race as occur in many individuals at once. If the same variation occurs in many animals simultaneously, there is a likelihood of similar individuals breeding together and thus perpetuating their characters. If, however, we assume that a certain variation appears in many individuals simultaneously we give up the idea of fortuitous variation and make the variations determinate. In doing this, as we have already seen, we give up natural selection as the cause of evolution.

With this fact in mind we can see the significance of the discovery of variations around a mean, for here we find a series of facts by which this difficulty of disappearance by cross-breeding is largely removed. When we recognize that all individuals are either above or below the mean in regard to any character, the action of natural selection becomes simple. Imagine for instance that conditions of food supply are such as to make it an advantage for a bird to have a long beak. It is true that any single variation producing a long beak would have little or no influence upon the species. But our study of variation has shown that most of the birds of the species have beaks either longer or shorter than the average. If four fifths of the birds must perish during some period

of famine, it is clear that the fifth that succeeds in living will be sure to contain more long-beaked birds than shorter ones. Now these animals must mate with each other and thus there would be no opportunity for the new character of longer beaks to be eliminated by cross-breeding. We have in short found that normal variations offer exactly the condition which has been theoretically demanded, viz., many simultaneous variations in the same direction, and this, too, without any suggestion of variations determined along definite lines by internal forces. As a result of such a condition the next generation will have a beak whose average length is longer than the average of the last generation. Evolution thus acts upon general averages and not upon individual variations. Advance is an advance of a species *en masse* and not by isolated spurts.

It is clear, further, that an advance by general averages will soon reach a state of equilibrium. The beak of the bird, for example, will not go on lengthening indefinitely, because after a time a length is reached where any further increase would be a disadvantage. When this time arrives natural selection will simply eliminate such individuals as depart most widely from the general average. Now such few observations of the actual working of natural selection as we have are of exactly this character. Most species appear to have reached a condition of equilibrium. When the struggle becomes severe we find that the extreme variations from the normal are eliminated, but when the struggle is lessened, the extremes have an opportunity to survive. The

English sparrow introduced into America, where its enemies are reduced and its struggle less severe, begins to show at once the survival of wider variations than in its native home. This probably means that the extreme individuals have had a chance to live because of the relaxation of the severity of competition. When the heavy stress of weather comes it is the extreme variations that suffer and die while the average birds live. This has been determined by observation and not simply by theory. Studies of a similar nature in snails and in crabs have yielded somewhat similar results, although the number of instances where the subject has been studied are, as yet, few. But these illustrations show forcibly the significance of variation around mean types. Under present conditions there is a certain average character preserved. But if the conditions change another average might be best fitted for the struggle and natural selection would soon bring the type to the new mean. Where the average is best fitted to the conditions the extremes will be the ones to yield in the struggle for life, but when this average is no longer adapted to the conditions of life, the forms above or below the average will be protected, and thus the mean character slowly change to a new position of equilibrium.

As already noticed in the last chapter, this principle of averages explains how characters of really slight value may be preserved by natural selection. If an organ is useful we may always expect to find amid its variations some individuals with the organ more developed and others with it less developed

than the average. While we may hesitate to think of slight changes being matters of life and death, it is quite easy to believe that in times of stress and severe competition, when perhaps nine tenths of the individuals must die, the tenth that lives will be more likely to be among those with this slightly useful character best developed, always provided other factors are equal. This would be all that is needed to place the character in question within the reach of natural selection. In short, the conception of variations as occurring on either side of a mean, and of natural selection acting upon averages, has made the whole action of natural selection much clearer. While this idea has been recognized for a long time it has in recent years been brought into clear light as the result of direct observations upon variations as they occur in nature. The matter is dwelt upon at some length here since a majority of those who talk about natural selection think of the law as acting upon isolated favorable variations and naturally see many serious obstacles to the theory from this standpoint. The law assumes quite a different aspect when we think of its acting as here described.

Of course it is plain that such considerations only apply to the problem of the growth of an organ or a character in size and efficiency. After an organ has become well enough developed to be of the slightest use it will always happen that some individuals will have it more and some less efficient than the average. It is equally manifest that this principle of averages does not explain the beginnings of organs.

For example, if the ancestral vertebrate possessed paired appendages large enough to be used for any purpose, this principle may be used to explain their modification in size and their development into fins, arms, wings, legs, etc. But it does not account for the *origin* of the original appendages, if an ancestral vertebrate ever existed without them. But the question of the origin of organs must be considered by itself later.

### *Is Evolution Continuous or Discontinuous?*

We may next ask whether the evolution of species has always been of the character above mentioned, viz., resulting from the selection of slight departures from the normal, or whether it may have ever been of a spasmodic character actually producing new types at a single jump. This subject is of extreme importance in enabling us to understand the method of organic evolution. Indeed, the answer to the question will completely control our understanding of the method of the origin of species. As we look at the organic world to-day we see that species are not only adaptive but also *discontinuous*. By this statement is meant that animals and plants are divided into groups which we call species, and that these species are commonly separated from each other by gaps. It is true that occasionally two allied species may be found connected by intermediate forms; but as a rule such a connection is not found and the species are therefore discontinuous. Now this must mean one of two things. Recognizing

that species have come from common ancestors, we may suppose, first, that they have in the past been connected with their common ancestor, and therefore with each other, by numerous connecting links, but that these connecting links have been exterminated by the process of elimination. If this is the case species have really been continuous with each other, their present discontinuity being due to the extermination of intermediate forms. Second, we may suppose that the new species arose from the common ancestor by a sudden jump. It may be that there occurred at some time in the past a variation so great as to deserve to be called a "sport," but which was of sufficient value to be preserved by natural selection and which thus formed the starting-point of a new species. On such a supposition the new species arose at a single jump and species have been discontinuous from the first. One method is called continuous and the other discontinuous evolution.

Now it makes a decided difference in our understanding of the method of evolution which of these two processes we find to be that of nature. It is not simply a little matter of detail, but it makes a difference in our fundamental conceptions. That this is so may be seen from a few simple considerations. As we have seen, small variations are abundant on every hand. Variations in size and efficiency of organs are absolutely sure to occur among animals with such a certainty that we need ask for no explanation of them. Indeed, it would be impossible to conceive any other condition of things. Considering

the variety of circumstances, it would be as impossible to conceive two animals to be exactly alike as it would be to conceive a dice to fall always on the same side. For such little variations in size and efficiency, then, we need ask for no explanation, and if it proves that evolution is based upon such variations the demand for the cause of variations, the "origin of the fittest," becomes one of little or no significance. If evolution has been produced by the selection of the slight variations above and below general averages then selection is the force which guides evolution. If, therefore, we find evolution to have been continuous in the sense above referred to, the demand for the origin of the fittest disappears. Naturally this position is held by those who find in natural selection the sufficient agency in producing the origin of species.

But if, on the other hand, we find that evolution has been discontinuous the matter stands quite otherwise. If it should be found that the origin of species has been discontinuous, that the first individual of a species arose by a single extraordinary birth, that the characters which mark the species made their appearance by a single or a few variations of great extent, then we must admit that natural selection does not satisfy us. We must at once ask further questions. We must ask what caused such a large variation to appear suddenly. We must ask whether it appeared in a single individual or a large number of individuals at once. If we conclude that it appeared only in a single individual, we must ask how it happened that it was not soon eliminated

by cross-breeding, for we have already seen that, admittedly, a single variation in a single individual has little or no chance for preservation by natural selection no matter how valuable it may be. But if we conclude that the variation appeared in large numbers of individuals simultaneously, we have even greater difficulty in explaining what could have produced in many individuals at once such a large and momentous variation. These questions will certainly demand an answer if we conclude that evolution has been discontinuous. Each of these questions is difficult to answer and it is, therefore, clear that it is more than a simple matter of detail whether we conclude that descent has been continuous or discontinuous.

If we are to find an answer to this question it is plain that it must be found in the study of variation. If evolution has been discontinuous this means that very large variations must sometimes occur which may be the starting-point of new types of descent. If, therefore, we should find among individuals only small indefinite variations this would indicate that discontinuous variation is not the method of nature. In the study of variation, therefore, must be found the answer to the problem of discontinuity.

### *Are Variations Continuous or Discontinuous?*

It has been the conclusion of most of the followers of Darwin that it is the selection of the numerous minute variations which has constituted the force of evolution; that descent, in other words, has been

continuous. This is the most natural view, since such variations occur on every hand, and since large individual variations would apparently be eliminated by crossing, while the principle of the selection of variations above and below general averages would largely avoid this difficulty of crossing. But what are the facts which the observations of recent years have disclosed as bearing upon the problem of continuity ?

In the first place it is certainly the case that the majority of variations in nature are of the character which may be called minute and indefinite. All of the departures from the mean in the way of excess or diminution in efficiency, all departures from the normal size of organs above or below the average, all of those variations which are to be made out by the careful measurements above mentioned, all these, which comprise the majority of variations, must be placed in the class of minute, indefinite variations. For although some of these departures may be considerable they are not enough, except in rare cases, to constitute a real discontinuous variation or a "sport." It will be admitted on all sides that in all animals and plants, in all species and in all individuals, are to be found these minute variations of many kinds, indefinite in character, occurring simultaneously in many organs at once, but variations of slight extent, and so clearly unconnected with any special purpose that they may be regarded as "hap-hazard," and demand no more explanation than the irregular shapes of the rough stones found in a quarry.

But on the other hand it is an equally striking fact that not all variations are of this character. It has certainly not been the expectation of naturalists to find that great and sudden variations occur in any considerable amount or that they have played any considerable part in the process of evolution. The whole theory of natural selection, as conceived by Darwin and developed by his followers for a quarter of a century, was that it has been the selection of the numerous fortuitous variations which has produced the origin of species, and that the process has been therefore a continuous one. It is certainly quite a surprise to find that great and sudden variations not only do occur, but are really quite common among organisms. But such appears to be undoubtedly the case. As our naturalists have, in recent years, made search for such discontinuous variations they have found them in unexpected numbers.

The character of such sudden great departures from the normal type is of course extremely varied. Among animals they include such variations as the appearance of extra teeth, extra vertebræ, extra toes or extra joints in the toes, extra mammæ, extra segments in segmented animals, extra branches in the horns, extra horns, or the fusion of two horns into one, etc. They even include such peculiarities as extra heads. They include complete changes in color, sudden and complete modifications of color markings, changes from right to left-handed coiling, the appearance of completely hairless individuals among hairy animals (*e. g.*, dogs, rats), or hairy birds, etc., etc. The list might be extended almost

indefinitely. Among plants we find instances equally numerous. The appearance of eight petals where there should be six, the presence of pink azaleas upon plants commonly producing white ones, the growth of peaches upon nectarine trees, or nectarines upon peach trees, the growth of branches out of the ends of pears will sufficiently serve as examples.

The characteristic feature of these variations is that they are commonly not connected with the normal forms by intermediate grades. For example, the cockroach has normally five joints in its toes, but twenty-five per cent. of the individuals have only four joints. But we do not find intermediate forms with four joints and a fifth partly obsolete. Among eight-petaled tulips the individual flowers have either six or eight petals. There are no seven-petaled tulips with six well-developed petals and rudiments of one or two more which might lead gradually from the six-petaled form to that with eight petals. In other words, the evidence points to the conclusion that these large variations have appeared by one sudden change, and not by a large number of minute intermediate stages.

Now it is certainly true that many of these large discontinuous variations bear close resemblance to monstrosities. A theory of evolution based upon monstrosities would hardly be tenable. Monstrosities are commonly regarded as weaklings, and not as having any power of developing independent races. A three-legged form is certainly an instance of discontinuous variation, but no one ever assumed

that such a monstrous individual would ever be a factor in developing a new race. But that many of these discontinuous variations are really monstrous forms does not in the least diminish the significance of their existence. It is impossible to draw any line between variations so extraordinary as to be properly classed as monstrous and those which are simply very large normal variations. All variations are departures from the normal type, and it is impossible to say when a variation is large enough to deserve to be called monstrous. These large variations do occur, and they arise as single jumps and not by an accumulation of numerous intermediate steps. When a hairless rat is found living among ordinary rats, and no rats are found with a partial clothing of hair, the inference is a legitimate one that the hairless individual is an illustration of a sudden large variation. If such sudden large variations should be of advantage to the race, may they not be the starting-point of a new species? The facts exist, and the problem is to determine whether they really play any part in the process of organic descent.

The real question at issue is not whether these discontinuous variations are properly called monstrous, but whether they ever become the starting-points of new races. It may be that they are simply freaks, coming and going with each generation, and leaving no lasting impression upon the race. Individual variations, as we have seen, have little chance of preservation, and if these discontinuous variations are weeded out by cross-breeding, from

the fact that they appear only in isolated cases, it is clear that they can play little or no part in the process of descent. The natural assumption would be that most of them would fail to have any influence upon the race, since they would be only individual variations, and hence fleeting. This is certainly the natural conclusion from our knowledge of heredity and the influence of cross-breeding. But, on the other hand, it is possible that we are dealing with something deeper than a simple chance variation. From the fact that such a large variation should suddenly occur, such as the development of an extra toe or joint, we may be sure that some rather profound influence has been acting upon the animal, an influence which is more than such passing incidents as do determine the more minute variations. It is possible that this profound influence has so affected the nature of the individuals that, in spite of cross-breeding, the variations in question will remain persistent. It may be that the nature is so changed that the new character will enforce itself upon future generations, and that thus an individual variation could be the origin of a new race. We know that among men such "sports" do sometimes seem to have quite a lasting influence. Titian, for example, was the first artist in his family. But the artistic genius followed the family from this starting-point for some generations. In spite of the fact that such an individual must mate with others that do not have the artistic genius the character may remain in the family. Such genius is sometimes known to increase for a time with successive

generations, perhaps finally to decrease again and disappear. It is at all events possible that something of this sort may take place with these discontinuous variations among animals.

*Do Discontinuous Variations Originate New Types?*

It is very difficult to determine the answer to this question. From logical grounds such a result would be regarded as improbable. But at the same time there are certain facts which plainly point to such a possibility. In the first place these discontinuous variations sometimes occur under conditions that seem to make it extremely probable that they may be the cause of new types. For example, Bateson has described two different types of earwigs, one with long and one with short forceps (Fig. 7). The two types belong doubtless to the same species. They live side by side and doubtless breed freely together. But, in spite of this, the two types remain distinct, and a collection of individuals from the same locality will show them grouped around two means with very few individuals showing intermediate grades. Here there are apparently two distinct types living side by side. It seems here practically certain that the two types could not have arisen by the natural selection of minute steps, since both types exist in about equal numbers in the same locality, a fact which proves that each is

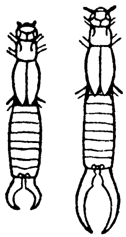

FIG. 7. Earwig—Two males with forceps of different length. (From Bateson.)

equally adapted to the conditions. Moreover, the presence of some individuals intermediate between these two types shows that all grades in length of forceps are perfectly consistent with the struggle for existence. Evidently we cannot assume that the two definite types have been derived by natural selection of minute stages. If not thus developed, there seems to be only one other possibility, and that is that these two types must be attributed to discontinuous variation, meaning by this that some unexplained law of variation produced at single births these two different types, and that once produced they remained distinct in spite of miscellaneous crossing.

Bateson gives another illustration which makes it at least probable that specific characters may have arisen by discontinuous variation. There are certain groups of Orthopterous insects in which the normal number of joints in the feet is four, while in others it is five, and one problem for the descent theory is to explain how in the former the five joints became reduced to four. Now, in accordance with the idea of natural selection, it would of course be necessary to claim that the production of the four-jointed from the primitive five-jointed condition was the result of the selection of many minute variations, and that for some reason in these special animals the reduction of joints from five to four was of such use to the animals that it eventually caused the survival of their lines of descent with the extermination of their five-jointed competitors. Such a position appears to be extremely improbable. In the first place it is hard

to believe that this character could ever have been of selective value. But, granting this possibility, we find that numerous five-jointed individuals are found living side by side with the four-jointed animals of the same species, a fact which practically negatives their production by natural selection alone. Secondly, it is clear that the new condition of four joints could not have been brought about by the selection of intermediate links, since intermediate links between four and five joints do not occur and are apparently impossible. The variation in question is not one which is open to fluctuation above and below a mean, and is therefore not amenable to the explanation of advance by variations around a mean. There are either four or five joints, clearly a discontinuous variation. When we find among certain species of cockroaches, for instance, many individuals with four joints and many others with five joints, living under identical conditions, we are debarred from believing that the differences are due to natural selection, and must attribute them to some laws of variation which produce sometimes four and sometimes five joints. But are we not forced to admit that the same facts apply to the production of four-jointed species from five-jointed ancestors? It is manifest that the probability, if not the necessity, is that the four-jointed species arose in the past by the influence of the same sort of discontinuous variations as occur to-day in the species which we can study in the living condition. If so we have, of course, an illustration of the production of specific characters, not by the accumulation

of minute steps by natural selection, but by the appearance of a large variation, a discontinuous variation, which, by some means, either through natural selection or otherwise, was retained in the race as a specific character. If we admit this position we have to reckon with discontinuous as well as continuous variations in explaining the production of species.

These two illustrations indicate the inherent probability that in some cases the discontinuous variations may have been the starting-point of new races and new species. But we are not wholly dependent upon inference for such a conclusion, for amid the various facts collected there are some, at least among domestic animals and plants, that prove the origin of new races by such sudden large variations. From the very nature of the case we can as yet expect to find such illustrations only among organisms under domestication. Animals and plants in nature have been too little studied to lead us to hope to find such instances among them. Indeed we should not know them if we found them. Only where a group of animals can be under constant observation for a considerable period of time is there a chance to observe the origin of new types by discontinuous variation. But among cultivated animals and plants they have been not infrequently found, and have been in some cases so striking that even in the earlier years of the study of evolution, before any systematic attempt was made to study discontinuous variations, such "remarkable births" were looked upon as a prominent factor in the origin of species.

The matter is of such importance in the understanding of the problem we are trying to get clearly before us that it is worth while to give several illustrations.

First may be mentioned the case of the Paraguay cattle. In 1770 a bull was born without horns. It was a discontinuous variation since its parents had horns. But although paired with ordinary cattle its offspring were hornless. This was clearly a case of a new variety starting with a single discontinuous variation, and, although the animals were forced to breed with ordinary mates, the new variation did not disappear by crossing as, theoretically, we ought to expect it would. Another well-known and even more extraordinary case is the appearance of the black-shouldered peacocks. It is a matter of historical record that this new type appeared as a discontinuous variation. In the midst of flocks of ordinary birds there appeared several animals of this new type. The strangest fact is that the same new type appeared at about the same time in several entirely disconnected flocks, indicating some common cause. This new type, like the last mentioned, was not eliminated by cross-breeding. The meaning of this case is not clear. Some naturalists have been inclined to look upon it as a reversion to an earlier condition. But however that may be, it was an instance of a discontinuous variation persisting in spite of cross-breeding. Another illustration is the appearance in Texas of a race of solid-hoofed hogs. In these animals the two central toes are rigidly grown together, the other two remaining distinct.

No one can say when this peculiarity arose or under what conditions. But there can be little doubt that it is a discontinuous variation, for there is no possibility of believing that the character was produced by the selection of many minute intermediate steps between this and the common form with free toes. But the variation thus appearing has become an established breed. The peculiarity is transmitted by inheritance, and there is no tendency to revert to the common type with free toes. The character is so completely a part of the nature of the animals that a cross between one of these solid-toed boars and a common sow produces offspring the majority of which show this character well developed and not in an intermediate condition. Here again do we find a discontinuous variation which has potency enough to hold its own in spite of the fact that it must have originally appeared in a single individual or a small number of individuals. If it appeared in a single individual its preservation cannot be explained by natural selection; if it appeared in several or a large number of individuals simultaneously its origin cannot be explained by fortuitous minute variations. Either horn of the dilemma indicates some other agency than natural selection of minute fortuitous variations as working in the origin of this race. A similar example is a family of cats observed by Poulton. In this family there appeared a female cat with an extra number of digits. This cat produced many families of kittens and their descendants were followed through seven generations. In all cases, of course, the probability is that the

females paired with males without this peculiarity. But nevertheless, during the whole seven generations, the large proportion of animals born showed the abnormal character of six or more toes on their feet. Here the variation was a discontinuous one, an entire toe making its appearance in a single individual. But it has such a hold on the animal that, in spite of cross-breeding, it has not disappeared, being retained to the seventh generation. It is certainly a discontinuous variation transmitted to posterity by heredity and its preservation has certainly not been due to natural selection. If selection could now come in and weed out the five-toed forms, a six-toed race would doubtless appear, and it would have started as a discontinuous variation.

Perhaps these examples should be classed as monstrosities. But this does not in the slightest degree affect the significance of the illustrations. Whether monstrosities or not, they have started new races, and they certainly show that some other factors besides the selection of minute fortuitous variations are concerned in the production of races. Some law associated with the production of variations and their inheritance lies at the bottom of such cases.

Even better instances may be found among vegetables. An excellent one is found in the Upright tomato. It is a variety of tomato differing in a large number of characters from other tomatoes, the differences being in many respects greater than the common differences between the different species of the family. The stem, the leaves, and the flowers are all strikingly different from those of the ordinary

tomato, and they are entirely sufficient to warrant a botanist who did not know their history to class them as distinct species. But the origin of the type is accurately known and even the man who sowed the seed from which the type suddenly arose. The seeds were those of ordinary tomatoes, but from them was produced, by some sudden variation, this widely different type. Now this type breeds its characters true by seed, and therefore has the one most distinctive characteristic of true species, or at least true varieties. Apparently there was produced here by a single step an entirely new type. Without insisting that this should be regarded as a true species, it is at all events an instance of a strikingly discontinuous variation, a new type appearing suddenly without any premonition, and certainly without any intermediate steps to lead to it from the ancestral form. The discontinuous form remained true and served as the starting-point of a new variety.

None of these examples are strictly to the point, since they concern organisms under domestication, and we cannot say how far artificial selection and artificial conditions have played a part in their origin. But they are sufficient to indicate that there may have been at work some forces in the production of species, besides the selection of such minute fortuitous variations as naturalists discover when they measure dimensions of organs or attempt to determine variations in their efficiency. Variations of a larger character and so suddenly produced as to be plainly due to some exceptional cause have

certainly played a part in the process; how large a part it is yet impossible to say. Whether the selection of minute variations has been the chief factor and the agency of these discontinuous variations has been the subordinate one, we need not attempt to decide. Most naturalists, certainly most supporters of the natural-selection theory, are inclined to believe that discontinuous variation has not been of much importance in the origin of species; that, while it may have occasionally been a factor in the production of new types, the chief cause of the origin of species has been the slow accumulation of minute variations. On the other hand, another school, of younger men, places greater stress upon these large changes, believing that in the origin of species there has been a swing from one point of stability to another and that, from the first, discontinuity is the rule. Their assumption is that minute variations count for little, representing simple oscillations on either side of a stable type, but that new species are commonly produced by a sudden assumption of a new position of stability. It is as if we had a solid with many sides. Tilting the solid up and down would represent the minute variations; turning it so it topples over upon another side would represent the formation of a new species.

Between such conflicting schools it is not our purpose to attempt to decide. Each admits the occasional significance of large discontinuous variations, and this admission brings even more forcibly to our attention the question of the origin of variations. These discontinuous variations are certainly not of

that slight character that they may be expected as the normal condition of things. They are more fundamental than variations in size and efficiency, since they sometimes represent the sudden appearance of a new organ at a single generation. While we need not especially disturb ourselves asking for the origin of the minute variations upon which natural selection is commonly supposed to act, it is plainly a different matter with these discontinuous variations. It may, in many cases, be a sufficient explanation of a given character, if we can say that it was developed by the natural selection of the most favorable among the miscellaneous variations which are constantly presented by animals. It is, however, not a sufficient explanation when we find such a character as that of the solid hoof of the hog, for example, appearing at a single step. With such cases we must ask a prior question and demand the cause of the variations.

It should perhaps be mentioned here that we have learned that single characters do not as a rule vary alone. Two birds will differ not only in the length of wing, but also in length of tail, legs, and, indeed, in many other points. We frequently find that several more or less closely related characters vary together. This fact is of considerable significance, since it enables us to understand how combinations of characters may be preserved. In trying to explain the origin of a complicated organ, involving the harmonious action of several parts, it is very difficult to imagine natural selection to act unless many parts vary together. For example, selection

could not preserve the large horns of a deer unless there appeared simultaneously a powerful neck to support the horns. If these two characters vary independently we can hardly understand it; for how can we imagine the deer to have developed the one character and then waited for the other? But the study of variation shows that many parts may vary together, and we can, therefore, easily see how selection may be able to act upon the most favorable combination rather than upon individual characters.

### *Discontinuous Variation as Explaining the Beginnings of Organs*

At one point this problem of discontinuous variations is of special significance, viz., in accounting for the beginnings of organs. From the very outset of the discussion aroused by the theory of natural selection, it has appeared that one of the most serious difficulties in the way of accepting natural selection as a satisfactory solution of descent is the seeming impossibility of accounting for the beginning of organs. Selection explains elimination and the moulding of organs to new functions, but it does n't explain origin. This difficulty appealed to Darwin and he candidly discussed it, suggesting various facts looking toward a solution of the difficulty. But the same question has been raised by nearly everyone who has discussed selection, and it has been studied from various standpoints. The usual answer to the objection has been that even at the outset organs have been of use for some pur-

pose, although, perhaps, different from their present purposes. For example, what is now used as a lung was in the beginning, before it was functional as a lung, of some value as hydrostatic apparatus among fishes. Or again, the beginning of the eye, as we have seen, was a pigment spot. These pigment spots were not organs of sight, but even at the very beginning they would serve to distinguish light from darkness, and thus be of use and within the reach of natural selection. The wing of a bat, it is true, is of no use as a flying organ until it is well developed, but it might have been of value at the outset in the same manner as is the fold of skin in the flying squirrel. Thus everywhere the answer has been that, even at the beginning, the organ may have been of some use for some purpose. But in spite of all that has been said it can hardly be claimed by anyone that the difficulties have been removed by one or all the considerations that have been urged. How an organ could ever get started is a mystery. It certainly cannot fall under the explanation of the selection of variations around a mean, for until an organ has made its appearance in some form it cannot show variations. In the study of evolution of fossils we get plenty of evidence as to the disappearance of organs or their modification into different structures for different purposes, but thus far paleontology has given us no knowledge of the actual beginning of organs.

In order to make a little clearer the real difficulty lying at this point let us consider an illustration, choosing for the purpose the evolution of the ap-

pendages of vertebrates. These appendages take the form of fins in fishes, of paddles in whales, legs in mammals, wings in birds, legs and arms in man, etc. Now it is possible to explain, by the principle of the selection of averages, the development of these appendages from one original type. Under the influence of the survival of the fittest these appendages may readily have become fins in the swimming fish, wings in the flying bird, and legs in the land animals. But upon the assumption that the original ancestor of the vertebrates was without appendages, an assumption which may or may not be true, what could have started the first appendage? Natural selection could not have preserved the rudiments of legs until such rudiments appeared, and what could have produced the first rudiment. It will be seen at once that the miscellaneous variations which we have been considering will not meet the case, since these are variations in the size and efficiency of organs already existing. Variations in organs cannot occur until the organ makes its appearance. Its origin must have been something new. When once the appendage became large enough to be of *any use whatever* its further development by natural selection can be understood. But what could have produced even a rudimentary useful appendage on the sides of a body previously smooth? It must have been a discontinuous variation. But this answer does not wholly remove the difficulty. First, we are again met with the questions already mentioned. If this organ appeared in one individual, what prevented its disappearance by

crossing? while, if it appeared in many, we must face the previous question of what caused the simultaneous appearance of a discontinuous variation in many individuals. Second, the types of discontinuous variation which we meet to-day help us only a little. When we find new organs appearing among animals and plants they are simply repetitions of parts already existing, *i. e.*, extra legs, etc. We do not yet find instances of absolutely new organs appearing, as must have been the case in the origin of the appendages. It is not a sufficient answer to this difficulty to say that, at the beginning, the appendages might have been used for an entirely different purpose and been very small. This answer is the one commonly given, but it really leaves their origin just as obscure. Nothing can come under the influence of natural selection until it gets started.

Various attempts have been made to meet this difficulty without resorting to sudden discontinuous variations, but without any real success. Slight variations on either side of a mean leading to the selection of averages cannot meet the problem. The appearance, upon either side of a spherical animal, of protuberances large enough to be of use for any purpose, indicates the sudden appearance of characters very different from the minute variations with which natural selection is supposed commonly to deal. Unless we admit that the variations which produce the beginnings of such organs are something more than slight changes in size and efficiency of organs, we cannot find in the simple natural selection of indefinite variations an explanation of the

origin of organs; if we do admit that variations are thus discontinuous and may produce a new organ of some size at a single step, then we cannot find an explanation of the variations in the indefinite miscellaneous influences which act upon animals. We must either find some additional force regulating the origin of species or some new factors explaining the appearance of variations.

This is more than a controversial position. It is true that much difference of opinion has been held over the alleged difficulty of accounting for the beginnings of organs and that the topic is ever under dispute. It is true that there are some naturalists who insist that the difficulty has been overrated. But it is at the same time true that no satisfactory method of meeting the difficulty has been suggested short of admitting the appearance of new organs, even though small and rudimentary, by single variations, which of course makes the laws of variation the real cause starting their evolution and not the law of natural selection. This fact has led some of our most thoughtful and observant naturalists to question seriously whether natural selection can be regarded as a *vera causa*, while it has convinced others that we can never find the explanation of descent by the study of natural selection, no matter how vigorously we pursue the subject, and that the only chance for further progress is in the study of the variations themselves. It has led our younger naturalists into researches in entirely new directions, as we shall see later. It has led to the growth of a distinct school of evolutionists in America, called

Neo Lamarckians, and it has even led Professor Weismann to a position in which he admits the inadequacy of natural selection to meet the problems. Professor Weismann, for reasons to be presently noticed, has become one of the leading exponents of the natural-selection doctrine, but even he has frankly admitted that "we must seek to discover why it happens that the useful variations are always present." He quotes with approbation the reply made to him by a breeder of animals, in answer to the question whether by selection he could produce any given type of animals. After careful thought the answer was that he could if the animals would furnish him with a start in the form of a proper variation. Selection cannot start the process of evolution. With all this testimony it is evident that minute indefinite variations on either side of a mean, leading to the selection of averages, does not account for the beginnings of organs.

### *Are Variations Determinate or Hap-Hazard?*

Unless we can assume that there are some predetermining forces regulating the appearance of variations in definite lines we should expect that such variations would be indefinite and irregular. Natural selection does not induce variations in definite lines, it simply preserves some variations at the expense of others. Hence, if variations do *appear* in definite lines, selection is no explanation of the origin of species. A stone picked up amid a mass of fragments is no more likely to be of one shape than

another, and if we pick up a hundred stones we should expect to find an indefinite number of shapes. If, however, we should find that each of this hundred stones, or a large majority of them, had a tendency to assume a certain somewhat definite shape we should say at once that there was a definite reason for it. If we should throw into a lake all of these hundred stones which were not flat, we should of course have only flat ones left. Our choice in throwing away some stones would then explain why only flat stones remained in our hands, but it would not explain why there were so many flat ones at the start. If the majority of these stones showed smooth, flat surfaces, we should perhaps explain it by the fact that the rocks were originally deposited in layers and that this stratification has controlled the shape of the fragments. It would then be the forces of stratification that determined the shape and not our selection. Thus, if we find the fragments all tending to assume some definite shape, we should find the explanation, not in the force of selection, but in some definite set of conditions which produced the fragments.

Now, applying this illustration to variations among animals and plants, we conclude that, if the variations are due to miscellaneous agencies acting haphazard, they should be indefinite in shape and extent. We should expect to find them just the sort of indefinite variations upon which the attempt has been made to found the doctrine of natural selection. But if, on the other hand, we find that variations have a tendency to show a likeness in many animals,

if they appear in certain organs and not in others, if they appear, generation after generation, of a similar nature, or if they appear in many successive generations running along the same lines, then the problem changes. The variations would then be determined by some prior law, and we can no longer be satisfied with the statement that variations are fortuitous, or with the assumption that the origin of species has been by the selection of chance variations. If variations arise in a definite manner they must be controlled by definite laws. If the same variation appears generation after generation it must be brought about by a common cause. If they appear in certain organs and not in others this must mean that certain definite forces are at work which affect some organs but not others. If for a long series of generations variations appear in the same direction, which natural selection may secondarily preserve, then it is clear that prior to the force of selection, we must look for some agency controlling the production of variations along definite lines. *If variations are definite then selection is not the fundamental cause of evolution.*

Now the study of animals and plants leaves hardly a possibility of believing that variations have been wholly of that " hap-hazard " character that has been sometimes assumed. If the black-shouldered peacock appeared independently in several localities at about the same time, we cannot believe that it was a hap-hazard variation, but must assume that some definite law was involved. Perhaps it was a reversion to an earlier condition, but certainly something

besides chance is needed. The fact that six-toed cats appear frequently, and that six-fingered men are not uncommon, points again to some controlling fundamental cause. But of more significance than these facts are others which have extended over much longer periods of time. For example, the development of the eye above described must have taken a very long period of time, how many thousands of generations we have no conception. Now such a development could never have occurred unless during all this period there was constant tendency toward variation in the eyes in a somewhat definite direction. The example is made more forcible by the fact that similar eyes have been developed independently at least twice in the animal kingdom. The eye of the vertebrate is, in its general structure, very similar to the eye of the squid. They are, however, sufficiently different to show that they have no genetic connection with each other, and the relation of the squid and the vertebrate is such as to make it positive that the one could not have been derived from the other. They have had an independent origin and development. But nevertheless the eyes of the two groups are so similar in structure that we cannot understand their origin unless we admit a tendency, in widely different groups of animals, to vary in somewhat similar directions. It cannot be claimed that this is the only type of visual organ possible, for the insects have developed a radically different one. Thus the presence of two such similar organs, independently developed, tells certainly that there has been a

tendency to vary in similar directions, *i. e.*, *determinate variations.*

The loss of the toes of the horse may be mentioned as another illustration. The gradual reduction of the number of toes from five to one in the horse and two in the ox, has been followed step by step among fossils. This reduction took a very long time, many thousands of years and thousands of generations being required to accomplish the result. Now it is clear that during this long period variations of a proper character must have been constantly appearing for natural selection to act upon. Variations in the line of reduced toes must have appeared generation after generation. Why should there have been ever present variations in the direction of reduced size, unless it be that variations have a tendency to run along definite lines ? A better illustration still is the development of the teeth of mammals which has been followed with care through the geological ages. In this development of teeth a very definite line of growth has been made out. Beginning with a simple conical tooth there have appeared upon the crown one tubercle after another. The appearance of these tubercles has always been in definite order, and so strictly is this order adhered to, that geologists have found it possible to predict with accuracy what sort of teeth will follow those of any particular animal in the history. The appearance of these cusps seems to be predetermined in the nature of the animals and thus represents a typical illustration of a determinate variation.

In a different line we find illustrations of the same

principle among plants. We find them here more readily than among animals, since plants have been more carefully observed. One of the best illustrations is found in the tomato plant. The Mikado type of tomato differs from other types in several different respects. It has fewer but larger leaves, with entire margins. It has decurrent stems and in other respects it is far removed from ordinary tomatoes. Now we not only know when this type arose, but we have historic evidence that the same type made its appearance in several independent instances. It first appeared in the "Keys Prolific," then in the "Nesbit Victoria," and later, in recent years, in two independent varieties, the "Mikado" and the "Potato-Leaf" tomatoes. Now this variation is a very large one, and there can be no question of its appearing by the accumulation of many intermediate steps. It is a discontinuous variation and, since we see it appearing in several independent instances, it is clearly inadequate to account for it by "fortuitous" variation. There must be something in the nature of the tomato or the laws of variation which has determined the constant reappearance of this important type of modification. In still another direction does the tomato illustrate the same principle. During the present century the whole family of tomatoes has been undergoing modification. The earlier small, erect plant with small fruit has been steadily moving forward into a new type with weak, spreading stems, large fruit and many other new and profound modifications. Of course modern varieties are numerous, but in these particulars they

all represent departures from the original type along rather definite lines. The forward movement has affected the whole group of tomatoes. Now there is no suspicion here that the progression has been due to inheritance from a common type. The original tomato from which the modern varieties sprung, has none of these characters. They have been independently acquired by various types, by selection or otherwise, but they certainly show that there has been a tendency for variations in this group of plants to follow definite lines. If we study a different species of plant the history is totally different. Among lima beans, for example, there has been a tendency to produce dwarf varieties and three dwarfed forms have arisen independently from three distinct types of beans. In other lines the same principle might be followed, showing that the direction of variation, and hence of selection, is predetermined in some way in the nature of the plant, and cannot be regarded as occurring in every direction and hence as "fortuitous."

An illustration of a different character may be found in the comparison of American trees with their nearest European allies. The American trees have leaves that fall earlier in the autumn and are less deeply toothed. The buds are smaller and the trees more diffuse but with fewer branches, and the seeds are smaller. Now these differences are general and apply to a large number of trees of widely distinct orders and growing in widely different stations. They are general differences between American and European trees. The fact that so many

independent species of trees have acquired these common characters, shows that some uniform influence has been at work determining the variations along definite lines. Whether these characters are inherited or not is a matter of importance to be considered presently.

It should be noticed that these considerations in regard to variations along definite lines have less significance in connection with such characters as can be supposed to advance by general averages. Some organs have been advancing in definite directions for long generations, but if the advance consists in an increase or decrease in size of the organs there is not needed any law of determinate variation to explain the matter. If it be an advantage to have an organ increase in size, and if variations in this organ occur around a central average type, then without any necessity for supposing a special law directing variations, we can understand how natural selection will continue to modify the species so as constantly to increase the size of the organ in question. Upon the theory of probability there must always exist individuals with the organ in question larger than the mean, and this is all that is needed. But, for characters whose development cannot be explained by the selection of variations around a mean, the explanation is hardly sufficient. Here again do we find the question of the origin of organs coming to the front as a difficulty. To explain the origin of organs it would seem that some sort of determinate variation is necessary.

## *Determinate Variation Produced by the Environment*

There is one series of factors which it seems most natural to call upon to explain the appearance of variations along definite lines. It is an explanation which in its origin antedates the doctrine of natural selection, and one which has occupied a very prominent place in the discussions of recent years. It is a factor recognized by Darwin and studied by him with his usual carefulness, but one which in recent years has been on the one hand advanced to a position far above that in which Darwin placed it, and on the other hand absolutely denied as having any influence at all. It is a factor which at first sight appears to furnish just what is lacking to the doctrine of natural selection, inasmuch as it explains determinate variation and the appearance of variations where they are needed.

To explain determinate variation there is needed some force acting upon organisms in a uniform manner. Such a force is found in the action of the environment upon the individual. In the environment we have a force which acts upon many individuals simultaneously, and upon all individuals of the same species in the same locality in essentially the same way. We have a force, moreover, which continues to act upon generation after generation and might be expected to produce similar influences upon successive generations. Moreover, it is a force which produces modifications in special organs needing them and not simply hap-hazard variations.

Apparently we have here just what is needed to supply the deficiencies of selection.

These factors are of several kinds. Foremost among them stands the influence of use and disuse, the direct action of food and climate, and the influence of effort on the part of the individual. Together these factors form the *Lamarckian factors*, although use and disuse are more especially the distinctively Lamarckian factors. The essence of the theory which involves these factors is that the environment influences first the individual, and that the modifications thus produced are transmitted to posterity through heredity. Variations in the individual are produced by the influences upon him of varying environment. Use increases and disuse decreases the size of organs; changes in climate and food always produce some important effect upon the structure of an animal or plant. Variations are thus brought about by the environment, and, since variations are the building stones of evolution, it is in reality the effects produced by changes in the environment that constitute the real cause of evolution.

Of the influence of the environment upon the individual no one has any question. The influence of use of an organ in increasing its size is seen every day, as for example in the growth of the blacksmith's arm. On all sides too do we find the effect of food shown, in stunting growth if it be scanty and in stimulating it if it be abundant. The effect of climate is equally evident, as witness the darkening of the skin of the European under the tropical sun. Certainly nothing is better attested or more

fully appreciated than the effect of the environment to produce modifications in the individual.

The question whether such influences affect the race is, however, quite a different one. There is no reason for thinking that the blacksmith transmits to his child any larger muscles from the fact that he has developed his own. However much his arm may have grown by use, his child inherits no advantage from it, but must begin life with the same kind of arm which his father had at birth. In this case the effect of use is not, so far as we can say, inherited. Now, although in such cases there is no reason for believing that the effects of use and disuse are inherited, still from the very beginning of the century, when the idea was advanced by Lamarck, it has been believed that the effects of use and disuse do eventually have an influence upon posterity. Lamarck was the first exponent of evolution in anything like its modern form, and he based his theory almost wholly upon the effects of use and disuse handed down to posterity by heredity. Darwin recognized the same principle and regarded it as an important factor contributing to the origin of species, but regarded it as of little influence compared with the more potent agency of natural selection. But in the last two decades certain American naturalists have brought this factor prominently to the front again, and have placed it foremost among the factors contributing to the formation of species. These naturalists constitute the Neo-Lamarckian school.

There are certainly many phenomena in nature

which would seem to receive a ready explanation in accordance with the idea of the inherited effects of use and disuse, and which are apparently unintelligible upon any other basis. For example the high development of the running muscles of the antelope, or the springing muscles of the lion would be readily explained by use, while the loss of eyes, by animals living in caves where eyes cannot be used, would readily come under the explanation of loss by disuse. Moreover, these Lamarckian factors would meet the requirement of furnishing variations where they are needed. Manifestly if use can produce variations they will occur in the organ used, and the variations will thus appear where needed and have a direct relation to increasing the efficiency of the organ. If disuse causes the degradation of an organ similar variations in the line of degradation would appear generation after generation, so long, in fact, as the organ fails to be used or until it disappears. Such variations would thus be in a definite direction and continued for many generations. They would, indeed, be *determinate* variations. They would exactly meet the demands which we have seen must be met by a theory of origin of variations. If the effects of use and disuse are factors in producing variations, we can understand how the outer toes of the horse's foot continued to grow smaller by disuse, while the inner one grew larger by use, and how this progressed age after age. Use and disuse would thus furnish the long-continued variations in definite directions. The direct effect of the environment

would furnish an explanation why many animals might vary independently but simultaneously in the same direction. For example, the climate and food would furnish a ready explanation of the marked difference between American and European trees mentioned above.

If use and disuse be real factors in evolution their influence would be great, even though the variation transmitted to the child in a single generation should be very small. Since variations produced by use would be in definite lines and in places where they were needed their effect would in time accumulate. The use of a part would thus be an influence determining the appearance of variation, and natural selection would be greatly assisted by the appearance of variations along lines where they were needed. Evidently these Lamarckian factors will aid us in finding the solution of some of the difficulties which we have found in the way of natural selection, provided the Lamarckian factors be real factors in nature. But the question has been recently forced to the front whether they are real factors at all, and whether they play *any* part in the origin of species. After being recognized and generally accepted for nearly a century they are to-day all regarded with scepticism. It is evident, in the first place, that however much the effects of use and disuse may aid us among animals, they are of little significance among plants, since plants are not active and neither use nor fail to use their organs. Now we find organs increasing or decreasing according to their usefulness among plants just as truly as among

animals. The loss of stamens in a pistilate flower is just as difficult to explain as the loss of the horse's toes. But the loss of the stamen could not have been due to disuse, since the stamens are purely passive in the life of the plants. There are hundreds of other instances that might be given where organs which are of no real value disappear, but which are not used in any active sense even when present. It is a question, therefore, whether we have really improved our position very much by discovering a factor which may be supposed to act in explaining the loss of organs among animals, but fails to account for similar phenomena among plants.

But are these Lamarckian factors real factors? If the effects of use and disuse have any influence upon the race they can only perpetuate these effects by being inherited. If these variations in the individual are transmitted to posterity they have an important influence upon descent; but if they are not inherited they can play no part in the origin of species. The question of the efficiency of the Lamarckian factors thus resolves itself into one of heredity, and we must postpone the further consideration of variation till a later chapter and turn our attention for a little to the study of heredity.

Fifteen years ago it appeared as if the doctrine of natural selection was about to be partly abandoned and its place filled by some other forces regulating the descent of organisms, the Lamarckian factors occupying a prominent position. The various objections against natural selection, some of which we

have already mentioned, were realized, and were regarded by a growing number of naturalists as so strong as to make it almost impossible to accept natural selection as competent to explain all the phenomena of the formation of species. If one had ventured at that time to make a prediction, it would probably have been that the next step in the history of the evolution doctrine would be the substitution of some other factor in the place of natural selection of fortuitous minute variations. Certainly no one would have predicted that the next step would be the re-establishment of the doctrine of natural selection upon a stronger foundation than ever, and the attempt to raise it into such an exalted position as to deny the existence of any other factor, making it not only efficient but sufficient. But such was the case. Fifteen years after the death of Darwin his principle of natural selection had been put upon a new foundation and raised to a position where Darwin never conceived of its being placed.

This change was brought about by the study of heredity, and with the appearance of a short essay by August Weismann in 1883 entitled, *On Heredity*, was inaugurated a new era in the study of biological science. This date was almost as important in modifying methods of thought and lines of experiment as was the date of the publication of Darwin's *Origin of Species*. Certainly no biological theory since the promulgation of the doctrine of natural selection has had such a stimulating effect upon biological thought, as the new ideas arising out of the consideration of the theories of Weismann. This much

must be admitted, whether or not we admit the truth of these theories.

### *Summary*

Variations are the building stones out of which the organism has been constructed, but, until the last fifteen years, they have not been seriously studied. Now that more attention has been given to them we have learned some facts that Darwin did not understand. We have learned that variations, *i. e.*, departures from the normal type, are extremely abundant. Not only are they very numerous in domesticated animals, but they are perhaps equally abundant among species living in nature. They occur in all organs and are of all kinds. They are commonly small, but are frequently of larger extent, a variation of nearly twenty-five per cent. in size being occasionally found. We have learned that these variations are grouped around a mean in such a way that, roughly speaking, half of the individuals are above the average and half below it in regard to any definite character. We have thus found that the facts of variation as they exist among animals point to a probable advance of animals upon the principle of averages and not by the selection of single variations, however useful. This has been, perhaps, one of the most important modifications which has arisen in our conceptions of evolution as the result of the actual study of variation.

But we have also learned that variations are not all of this character. We have seen that, whether or

not evolution has been continuous, certain it is that variations are frequently discontinuous. Besides the slight departures from the mean type, variations are constantly occurring of such profound significance that we commonly call them "monstrosities" or "sports." But whether they are really to be called monstrosities or not is comparatively unimportant, since there appears to be good reason for believing that occasionally they are the beginnings of new races and therefore possibly of new species. The study of variation, in other words, has indicated that discontinuous variation may be a factor in the method of the origin of species. Whether they are an important or an unimportant factor has not yet been settled, naturalists being still in disagreement in regard to this question.

We have learned further that there appear to be good reasons for believing that variations are "determinate," occurring in definite lines and therefore controlled by some forces prior to selection. While this conclusion is hardly capable of demonstration it is a very general conviction that such is the case. In asking for the cause of determinate variation, we have noticed that in the action of the environment upon animals and plants we have a constantly acting agency which might be supposed to be adapted to produce just such variations along similar lines for long generations together. The environment acts upon many individuals alike and may be supposed to produce similar results in them. Moreover the environment, using the term to include use and disuse as well as food and climate, will produce

variations in organs where changes are needed to adapt the animal to its conditions. The environment seems therefore to be an agent such as is needed for the explanation of determinate variations. But whether or not it is such an agent we have seen to depend upon whether the effects produced by such external agencies are transmitted to future generations, for if they are not they cannot play any part in the process of evolution. This has brought us to the question of heredity which also involves the question of the origin of variations.

# CHAPTER V

## HEREDITY

HEREDITY is the link that binds the successive generations together. It is this which makes it possible for one generation to benefit by the acquirements of the preceding generation. Were it not for heredity each generation would be obliged to begin its evolution anew. But heredity holds the characters which one generation acquires and hands them down as a legacy to the future. Each generation receives a legacy to which it can add, and thus the process of evolution can go on by accumulation. Heredity has always been recognized as a fact and it is no more palpable to-day than it was two thousand years ago; but, as the subject has been studied in the light of the descent theory, it has been assuming in the last fifteen years a very different aspect from that which it has had during previous centuries.

### *Acquired and Congenital Variations*

Before taking up the modern theories of heredity which lie at the bottom of present day biological discussion, it will serve to make the bearing of the

matter clearer if we distinguish in our minds two different kinds of variation among animals and plants, viz., *acquired* and *congenital* variations. A distinction between these two types of variations has indeed been clearly enough recognized by Darwin and all his students. It was this distinction which, in large measure, made the difference between his views and those of Lamarck. But in spite of the fact that they were distinguished in earlier years it was the theory of heredity advanced by Weismann which, for the first time, brought these two types of variation into such bold contrast that the radical distinction between them was recognized.

Acquired characters are those produced in the individual by the direct action of the environment upon him as an individual. The term is a very poor one, since all characters, even those that are congenital, must have been acquired at some time; but since the phrase is in common use, we will employ it in this discussion. Congenital characters, on the other hand, are those which the individual inherits. The distinction between these two types of characters is theoretically sufficiently clear, although it is not always easy or possible, in practice, to distinguish the one from the other. Acquired characters are the result of the action of external conditions; congenital characters, the result of internal conditions. Acquired characters, therefore, include all such as result from the effects of use and disuse, as the result of mutilations, of the action of climate upon the individual, or as the effect of changes of food, etc. Congenital characters will include

anything which an animal inherits from its parents, or any character which is born in the individual. It is not necessary that a congenital character should be apparent at birth, for many such characters appear only in adult life. For example, a child may inherit black hair from his father, but this black color appears only after several years of life have passed, the color of the hair during childhood having been light. This, of course, makes it frequently difficult to determine whether a given character is congenital or acquired. If a man learns to use alcoholic drinks and develops a strong appetite for alcohol, how are we to tell whether he developed the appetite because he acquired the habit of drinking, or acquired the habit of drinking because he had an inborn appetite for alcohol? Further, there is a difference between congenital and strictly inherited characters. A hereditary character must be present in the parent and transmitted to the offspring. But a congenital character need not be present in the parent. It may frequently happen that some influence affects the germinal substance from which an individual is sprung in such a way as to produce in him characters which his parents did not have. Such characters would of course be part of the nature of the individual when born, although not properly inherited from the parents, and they would, therefore, be truly congenital. This makes it still more difficult to distinguish in practice between congenital and acquired characters. For how is it possible to say, in regard to a character which appears for the first time in an individual, whether it

is one which has been produced in him by the direct action of the environment upon him as an individual, or was due to some modification in the germ substance from which he sprung and is hence congenital? This difficulty in distinguishing between the two classes of characters has had, as we shall see, a very important bearing upon problems of heredity, but the difficulty of recognizing them does not make them any the less distinct.

An individual may be said to begin his existence at the moment that the egg from which he develops is fertilized by the spermatozoön. Now the influences which determine what characters the individual shall have must either be previous or subsequent to that moment. If they are previous to the fertilization they affect, not the individual directly, but simply the germinal substance (egg or spermatozoön) from which he is to develop, and, so far as the individual is concerned, they are congenital. If they exert their influence after the fertilization they affect the individual directly and are "acquired." Now, while these two types of characters were recognized in the discussions which preceded the theories of Weismann, it is certain that before that time they were not so sharply separated from each other as having radically different relations to the problem of descent. The distinction was looked upon as one of degree rather than of kind. All through the writings of Darwin and his followers we find variations very generally attributed to changes in climate and environment, and such changes, since they affect the individual directly, are *acquired*. We also find

the statement that animals are born with an inherent tendency to vary, and these variations are congenital. Each of these types of variation has been accepted as contributing to the general process of descent. But Darwin founded his theory largely upon congenital variations, while Lamarck based his upon acquired characters. Darwin said that organic evolution was produced by the selection of chance variations most of which were congenital. Lamarck, and the more recent Neo-Lamarckians, say that evolution has been produced largely by the preserved effects of the environment upon the individual. Darwinism is a theory of descent *with selection*, and Lamarckism a theory of descent *with modification.* Up to the time of Weismann the distinction between these two theories was largely one of degree, each admitting both factors. Since the time of Weismann, however, the two types of variation have been sharply distinguished and the relation between the two theories is nearly one of exclusion. The Weismannians absolutely deny the Lamarckian factor, while the Neo-Lamarckians relegate the factor of natural selection to a very subordinate position. The cause for this radical distinction is found in the theory of heredity advanced by Weismann. We must therefore leave for the present the discussion of the factors of descent and consider in some detail the new theory of heredity.

### *Weismann's Theory of Heredity*

For a century or more scientists have been advancing various theories of heredity. It is really

the greatest marvel of nature that a child should be like its parents. The attempts to find an explanation of this marvel have resulted in the promulgation of many hypotheses and theories of heredity involving various degrees of absurdity. Even Darwin, with his great caution in advancing theories, formulated a theory of heredity which he called *pangenesis*. He felt forced to do this because it is so evident that the whole conception of natural selection, or, indeed, any theory of evolution, is manifestly based upon heredity. It is only such characters as are transmitted by heredity that can have any influence upon the process of descent. Some understanding of this phenomenon of heredity seems therefore needed before we can claim that we have made even a beginning in an explanation of the origin of species. This feeling has led to the suggestion of one theory after another as an explanation of heredity. In regard to most of the theories which preceded Weismann it may be said, however, that they may all be rejected as visionary, and it is doubtful whether they were ever accepted by any persons besides their authors. It is even doubtful whether their authors had much confidence in them. Remembering this, it is somewhat surprising to find that a new theory advanced by Weismann, not only received support from others besides its author, but, as we shall see, has become adopted with great unanimity as forming the true basis of heredity, even though many scientists feel it necessary to modify the theory in various respects.

The reason for this difference is twofold. In the

first place, the earlier theories were purely hypothetical, complicated beyond conception and demanding impossible drafts upon the imagination. Weismann's theory is simple and logical and appears to be a most natural explanation of the facts. Secondly, while the other theories have been pure hypotheses, unsupported by evidence, Weismann's theory has received very decided support from direct observation. Leaving all other theories out of account as of little significance to-day, let us turn at once to the theory of Weismann. The significance of the discussions of modern biology are so dependent upon a full understanding of this theory that it must be explained at some length. A better comprehension of the theory can be obtained if it be considered to a certain extent historically. The original conception of the theory has been very considerably modified by recent discoveries, but we can get a better appreciation of it as it stands to-day by noticing, first, its original form, and then considering the chief modifications that have been made. As at first propounded the theory was essentially as follows:

### *The Essence of Heredity*

If we consider the process of reproduction in the simplest unicellular forms, the problem of heredity explains itself. In such a case we have the whole animal made of a simple mass of protoplasm (Fig. 8), and its reproduction consists simply in dividing into two equivalent halves. When such a mass of

living matter divides into halves it is easy to see that the halves will be alike, since each is half of the same living cell. There is here no such thing as mother and daughter, and the likeness between the two individuals resulting from the division is a logical consequence of the process. When, however, a higher animal reproduces, the process is radically different. The animal does not divide into halves, but one single cell, a very minute part of the adult, is set apart to develop into a new individual. For the moment we will leave out of consideration the matter of sexual union, to be taken up later. This reproductive cell is the egg.

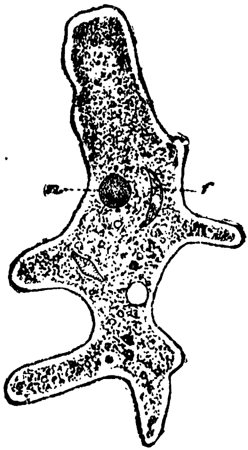


FIG. 8. An Amœba. A single cell without cell wall, *n* is the nucleus; *f*, a bit of food which the cell has absorbed.

This cell must be a very extraordinary body for, although we can say very little about the internal structure of the egg, this much is clear. Its internal structure must be such that potentially it may be said to contain the adult. Let us for convenience take a concrete case and say that the egg of a starfish contains potentially a starfish. By this we simply mean that its structure is such that when it is placed under proper conditions it will develop into a starfish, although a very similar egg placed under *the same* conditions would develop into a sea urchin. If these two eggs, placed under identical conditions,

develop, the one into a starfish and the other into a sea urchin, it is clear that the differences in the adults must be represented by corresponding differences in the eggs. Moreover, it is plain, for similar reasons, that all the inherited characters of the adult must be represented by corresponding differences in the eggs. Thus this single egg cell must have a structure representing in some way the whole starfish.

When an egg begins to develop the first step is the division into halves. Now just as we can understand how the halves of a unicellular animal are alike, since each is half of the same individual cell, so we can easily understand how each half of this divided egg may be like the other half. The egg has simply divided into halves, and, if the original egg possessed the power to develop into an adult starfish with certain definite characters, so each half can easily be understood to have similar powers, provided the division is such as to divide the hereditary material into two equivalent halves and does not divide it into two unlike halves. Now we can easily understand this process to go on indefinitely, division after division occurring, and, so long as the method of division remains the same, each resulting cell will have the same powers. It would be a repetition of the same process which we notice in the unicellular animal (Fig. 8), each cell will be like the other since each is half of the other. Therefore it would follow that if the original egg cell possessed the power to develop into an adult with definite characters, each of these divisions

should have the power of developing into a similar adult.

After a little, however, in accordance with the theory, there begins a new type of division. A *differentiation* among the cells begins to take place. The hereditary material in some of the cells no longer divides in such a way that the separate cells are identical, but in such manner that they receive

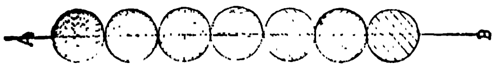

FIG 9.

different portions of the hereditary substance. As a crude illustration, imagine several beads in a line (Fig. 9), each unlike the others. If this string of beads is divided lengthwise (Fig. 9 AB) each half will be like the other and each like the original string, except of course in size, since each will contain half of each bead. If, however, the division occur crosswise, plainly the halves are no longer alike. One of these methods results simply in multiplication, the other in differentiation. Now, if we may imagine the hereditary characters in the starfish egg comparable to such a string of beads, we see that so long as the division of the cells was of a character comparable to the longitudinal splitting, the resulting parts will be equivalent, so far as hereditary characters are concerned. If, however, a division comparable to the transverse one should begin, then the resulting cells would become unlike; each one of them would receive only a portion of the hereditary characters.

The essence of the theory of Weismann is that at a certain period in the early-developing egg, the cells (or hereditary material) become separated into two parts. In one part the cells begin to divide by the process of differentiation as above described. This portion of the hereditary substance Weismann called the *somaplasm*, because it was now concerned in building up the body of the developing starfish. For the sake of simplicity let us imagine one half of the dividing egg (Fig. 10) is the *somaplasm*. According to the theory, this part now goes on dividing and becomes differentiated more and more with each division. As it divides, the newly formed parts are set apart to form the different organs of the starfish, some of them producing the digestive organs, some the arms, etc., and each part of course at the proper time receives just that part of the hereditary material which is concerned in the formation of the organ in question. In time this half of the egg

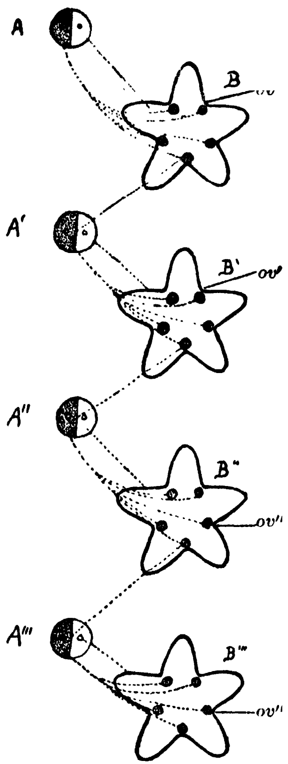


FIG. 10. Diagram illustrating the principle of heredity.

develops into the new starfish which arises from the egg (Fig. 10), and which we will call the second generation.

Meantime the other half of the egg (Fig. 10) has had a very different history. It retains the method of division corresponding to the longitudinal splitting, so that no differentiation of its substance occurs. Each of the cells which arise from this half, therefore, contains identical hereditary matter, and each of these cells will consequently possess the same characters as the original egg. If the original egg possessed the power to develop into a starfish with certain definite characters, it would follow that each cell resulting from this undifferentiated division would have the same powers. Now this half of the egg does *not* contribute to form the body of the second generation. It simply *remains inside* of the starfish that is developing from the other half of the egg. It thus happens that the new starfish has inside its body a certain amount of material, derived from the original egg, and which has not become changed at all during the egg development. Every cell in this material is identical in its powers with the original egg because of the method of undifferentiating division. The hereditary substance has increased in amount by growth, but it has not changed its character. Now this mass of hereditary cells in the body of the developing starfish is finally lodged in the ovaries. The ovaries thus come to contain a lot of cells which have been derived directly from the egg without differentiation. (Fig. 10. *ov.*)

Thus the ovaries of the new starfish contain large

numbers of cells which are not to be compared with the other cells of the body at all. They have been derived by direct descent, without differentiation, from the last egg and hence each possesses the same powers, so far as heredity is concerned, as that egg. The other cells of the body have lost this power of transmitting hereditary characters, since they have arisen by differentiating division. Now the cells of the ovary in time become eggs. When the starfish becomes adult one of the ovary cells is separated from the body as an egg (Fig. 10A′), and, under proper conditions, it produces a new individual. It is clear, however, that this new individual arising from the second egg will be like the first individual arising from the first egg, since, as we have seen, the second egg contains identical germ material, derived from the undifferentiated half of the first egg. Hence the third generation of starfishes will be exactly like the second. In the development of this egg the same process is repeated. Part of it develops into the body while the other part remains undifferentiated, dividing and growing however, and is finally stored away in the ovaries of the next generation. Evidently the animals of the second and third generation would be alike and we should doubtless conclude that the third generation had inherited from the second. But in reality the third generation has *inherited nothing from the second.* It is like it simply because it has developed from part of the same *germ plasm.*

In this way it is seen that the germinal substance is continuous from generation to generation. Each

individual carries around in his body a certain amount of this germ substance which is ordinarily stored in the reproductive gland. When a new individual appears by reproduction a bit of this germ substance is taken from the store to form an egg. In the development of the egg the germ substance multiplies and a new lot of it, identical with the old, is stored away in the ovary of the second generation. Heredity is thus explained. Successive generations are alike because they are controlled in their development by bits of the same germinal material. So far as concerns inherited traits therefore, each individual is rather a trustee than a testator. He receives some germinal material which he hands down to the next generation, but he hands nothing of his own accord.

### *The Essence of Variation*

There is no difficulty in thus understanding the likeness of successive generations. But plainly, in accordance with the theory as thus far developed, they would not only be nearly alike but *identical.* Coming thus from bits of identical germ substance there would be no possibility for any inherited differences. The only variations that would be possible would be such as were produced in the individual by the direct influence of the environment upon him. This, however, would be disastrous to any theory of evolution. It would make congenital variations impossible and would result in an absolute constancy of successive generations. An evolution of species would be impossible.

This difficulty is met by a second factor in the reproductive process. In ordinary reproduction among animals and plants the new individual does not arise from a single egg. Sexual reproduction is well-nigh universal among animals and plants, and is universal among all higher orders. Now, in sexual reproduction there is always a union of two different bits of germ substance, commonly derived from two different individuals. One of them is the *egg*, and the other the *spermatozoön*, or male reproductive cell. Both of these bodies contain germinal (*i. e.*, hereditary) material, and they unite with each other in the process of fertilization, so that the next generation actually comes from a bit of germinal substance derived from *two* different individuals. Now, if the two parents are in any degree unlike each other, the resulting offspring cannot be like both. He must be either like the one or the other or different from both. Inasmuch as the fertilized egg is composed of germ material derived from two different sources and mixed together, it is most probable that the resulting individual will be a compromise between the two parents. The mixture of the germ material will be unlike either of them alone, and hence the resulting individual will show congenital variations, *i. e.*, variations which are due to the peculiarities of the germ substance from which he was derived, and which will hence be born into his nature. Here then we find the possibility of an indefinite amount of congenital variation. Recognizing the differences that exist between individuals, and remembering that sexual union among most animals and plants

occurs now between one pair of individuals and now between another, it is evident that in no two cases will there be a likelihood of an identical combination of germ substance in any two individuals. Even if the same individuals do mate together repeatedly it is equally evident, considering the great complexity of this germinal material, that the two bits from the two parents will not be likely to unite in exactly the same way. When we mix two complex substances there is an almost infinite possibility of variety in the mixture. Therefore, in this process of combination of germ material in sexual reproduction there is an abundant opportunity for the starting of congenital variations. Sexual reproduction appears thus to be a phenomenon whose purpose in nature is to introduce variation and which has thus made evolution a possibility.

It is further evident that such variations will tend to be transmitted to the following generations. The germ substance which is handed down to the next generation is of course this mixture of germinal material, and if the mixture produced a variation in the first following generation, it would in a similar way affect all following generations. At each reproduction it would of course be sexually combined with another bit from a new individual, but a variation once in the germ plasm would be sure to influence all subsequent generations, unless some other combination should neutralize it. The germ substance being the basis of subsequent generations, any variation once incorporated in it will be transmitted to posterity. Congenital variations will therefore

have a strong tendency to appear in subsequent generations.

On the other hand, no variation appearing in the body of the individual, as the result of the action of the environment upon it, will be retained. It is only the character of the germ plasm that determines the inheritance of the subsequent generations. As we have seen, the body of the individual simply has charge of this germinal material, and no change in the character of the individual can affect it. A trustee might become bankrupt himself, but, if he were a faithful trustee, his bankruptcy would not affect the property which he held in trust. So since the individual is simply a trustee of the germ substance for future generations, no disasters which affect him, and no favorable conditions, can change the character of the hereditary substance which he hands on to the next generation. In other words, *acquired characters cannot be transmitted to posterity.* The significance of this conclusion, with its complete rejection of the whole series of Lamarckian factors will be noticed later.

The strength of this theory of heredity is seen at a glance, for it lies primarily in its simplicity. Nothing can be more certain than that the egg does contain some material substance which in some way determines the character of the individual that arises from it. Nothing can be more simple than to suppose that some of this substance is simply handed on from generation to generation, and that thus successive generations should be alike. Were it not for the somewhat surprising consequences in regard to

the transmission of acquired characters, it is almost certain that the theory would have been accepted without hesitation. Its very simplicity is almost a demonstration of its truth, unless cogent arguments arise against it.

It must be noticed that this theory of heredity was not wholly new with Weismann, although undoubtedly developed independently by him. Some years before a similar view of heredity had been advanced by Mr. Galton, and called the doctrine of "stirp." In some respects it differed from the view of Weismann, and it never took such a hold of biologists as did the theory advanced by Weismann. Almost at the same time with the publication of Weismann's essay appeared a theory of heredity by Professor Brooks which, in respect to the idea of the continuity of the germinal substance, agreed with that of Weismann. Brooks's conception was not, however, quite so simple as that of Weismann, and was burdened with certain factors which made it difficult to accept. While therefore the idea of the continuity of the germinal substance was not really new with Weismann, he has received, rightly or wrongly, the credit for the theory.

### *Modifications of Weismann's Original Theory*

That the theory is extremely simple will be admitted on all sides, but something more than simplicity is needed before it can be accepted. If the doctrine is true it ought to be possible to get experimental evidence for it. It ought to be possible to

determine whether the cells which are to form the ovaries *are* set apart early in the division of the egg and kept distinct from the rest of the cells during the subsequent development. It is easy to understand that the doctrine gave a great stimulus to the microscopical studies of the developing egg. These studies have had the result of bringing forward very suggestive confirmations of the theory of Weismann, but they have produced certain modifications of that theory, which have been found necessary to adapt it to the facts of development as they have been disclosed in the last fifteen years.

One essential change in the theory has consisted in pointing out more definitely the real germinal hereditary substance. The idea that a special cell of the segmenting egg is early set apart as an undifferentiated germ cell to form the reproductive bodies, is not found commonly to be true, although it does appear to be the case in a few animals. But such a condition is not necessary to the theory, and, indeed, recent discoveries have apparently shown us what part of the egg constitutes the real germinal substance which is continuous from generation to generation. This matter cannot be understood, however, without a knowledge of facts upon which the new aspect of the theory is based. These facts have been developed in connection with the modern study of the fertilization and development of the egg. It will be necessary for us, therefore, to review some of the most important results of this study, since they lie at the basis of all modern discussions of heredity.

When an egg is studied with the modern microscope it is found to consist of quite a number of parts. A diagrammatic representation of an egg is shown in Fig. 11. Of the parts there figured and named we need notice only three, since study shows these alone to be of special importance to the process of heredity and development. These are: first, the general substance of the egg, called *cytoplasm* (Fig. 11 *a*); second, lying within the cytoplasm a very minute body called the *centrosome* (Fig. 11 *g*); third, a material lying within the nucleus which assumes a variety of forms and is called *chromatin* from the fact that it readily absorbs colors (Fig. 11 *e*). This chromatin is sometimes in the form of a very intricate network (Fig. 11), or sometimes it appears as a long, endless thread, or it may appear as a number of short, separate threads. In the same cell the chromatin may assume different forms, but in all cells it appears, under certain conditions, to break up into a number of short threads called *chromosomes*, and the number of chromosomes

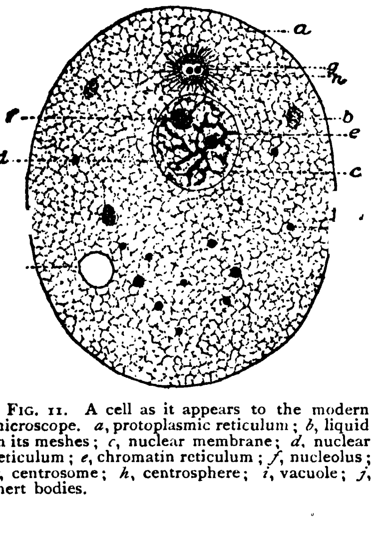


FIG. 11. A cell as it appears to the modern microscope. *a*, protoplasmic reticulum; *b*, liquid in its meshes; *c*, nuclear membrane; *d*, nuclear reticulum; *e*, chromatin reticulum; *f*, nucleolus; *g*, centrosome; *h*, centrosphere; *i*, vacuole; *j*, inert bodies.

is always the same for the eggs of any single species of animal or plant. The other bodies in the egg appear to be secondary to the process of heredity.

Now, in the preparation of this egg for reproduction, certain very significant changes take place within it, changes which are simply preparatory for fusion with the male reproductive cell. To understand these changes it is necessary to notice, first, that *all* of the cells of the body of the animal have parts essentially similar to those described, although the centrosome is apparently not always present in other cells. The chromatin material is always found, and always shows the same tendency to break up into a number of short threads at certain stages. The number of these chromosomes is always the same in *all* the cells of the body of any animal or plant. Some animals for instance always show four of these chromosomes when the network breaks up, others twelve, others a large number, but always the same for the species. The number is, however, just half the number of the chromosomes in the egg. If the body cells contain four threads, the egg contains eight; if the body cells contain twelve, the egg cells have twenty-four. The reason is that the egg cell doubles its number of chromosomes at a stage just preceding its final formation into an egg. Such a full-grown egg is not yet ready for its union with the male cell.

If, now, for a moment we turn our attention from the egg to the male reproductive cell we find something which at first seems very different. In such a cell we find at first no considerable amount of cytoplasm (Fig. 12), the only part representing this

large part of the egg being the spermatozoan tail (Fig. 12). We do find, however, a centrosome lodged somewhere in it, sometimes in a little piece connecting the head and the tail, and sometimes in the head; and we find in the head the same sort of chromosomes that we find in the egg. But the number, instead of being twice that of the ordinary cells of the body, is only half the ordinary number, and, therefore, just one quarter of the number in the egg nucleus. The egg is therefore not equivalent to the spermatozoön, since it has a much larger amount of cytoplasm and four times as many chromosomes. The egg is, however, not yet ready for union with the spermatozoön and now goes through a series of changes which make the two more nearly equivalent.


FIG. 12. A sperm-cell. *ce*, centrosome; *cy*, tail-cytoplasm.

The centrosome of the egg first shows signs of activity, becoming surrounded by a number of delicate radiating threads, and it soon begins to move toward the surface of the egg, accompanied by the nucleus. On its way it divides into two, each of the centrosomes thus formed passing to opposite sides of the nucleus (Fig. 14). One of the centrosomes now pushes its way out of the egg

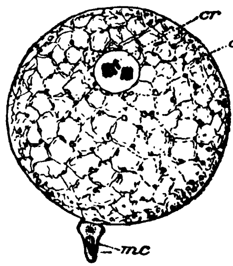


FIG. 13. This and the following figures represent the process of fertilization of an egg. In all figures *cr* is the chromosomes; *cs* represents the cell substance (omitted in the following figures); *mc* is the male reproductive cell lying in contact with egg; *mn* is the male nucleus after entering the egg.

and comes to lie in a little prominence on one side of the egg (Fig. 15). Meantime the chromosomes have been arranging themselves into two rows, possibly being pulled or pushed into these positions by the action of the fibres (Fig. 14). Next it is seen that the chromosomes forming the row next to

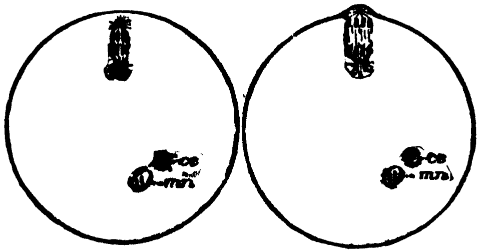


FIG. 14. FIG. 15.

FIG. 14. The egg centrosomes have changed their position. The male cell with its centrosome remains inactive until the stage represented in FIG. 19.

FIG. 15. Beginning of the first division for removing superfluous chromosomes.

the centrosome that has been extruded to the egg begin to move toward that body, thus separating from the other row which, in a similar manner, move toward the centrosome still remaining in the egg. In this way, after a little, one half of the chromosomes are eventually entirely extruded from the egg into the little protuberance formed around the extruded centrosome (Fig. 16), leaving the egg with a number only double that of the spermatozoön. After this there is a little pause, but soon the centrosome left within the egg divides again, each half passing to opposite sides of the nucleus, and again the chromosomes arrange themselves into two

rows. Again the outer centrosome pushes itself out of the egg into a second little protrusion (Fig. 17), and again the two rows of chromosomes separate from each other, one row passing into the second protrusion and the other remaining in the egg. The second little cell separates from the egg, and thus the egg is left with only one quarter of its original

FIG. 16. FIG. 17.

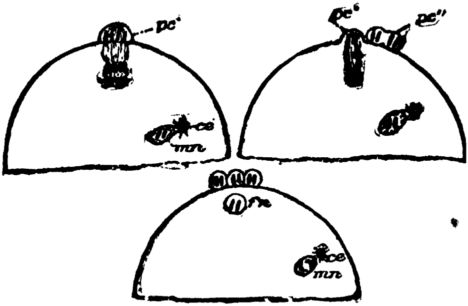

FIG. 18.

FIG. 16. First division complete and first polar cell formed, *pc.'*
FIG. 17. Formation of the second polar cell, *pc.''*
FIG. 18. Completion of the process of extrusion of the chromatic material; *fn* shows the two chromosomes retained in the egg, forming the female pronucleus. The centrosome has disappeared.

number of chromosomes, (Fig. 18) which is half the number found in the ordinary cells of the animal, but is exactly the same as that of the spermatozoön. Thus, so far as concerns chromosomes, the egg and male cell have been made equivalent.

Now as we study the development of the egg we find that these little protruded cells, "polar cells" as they are called, have nothing to do with the development of the adult. The egg proper, after uniting

with the spermatozoön, develops into the new individual, and these little polar cells soon disappear. Thus we see that, by the process described, the egg actually throws away three quarters of its chromatin, and reaches a condition in which it has exactly the same amount as the spermatozoön.

Next, the spermatozoön enters the egg carrying with it its centrosome and head, but leaving its tail outside. It may have entered the egg before this stage but remained dormant until now. After it enters we find, in some cases at least, that the egg centrosome disappears and thus the egg contains only the one centrosome which has been brought in by the spermatozoön. This centrosome now begins to show signs of activity, and it soon brings together the egg nucleus, with its remaining chromosomes, and the spermatozoön head containing its equal number of chromosomes (Fig. 19). These two masses of chromosomes, however, break up into a network and are then brought in contact near the middle of the egg. The centrosome now divides into two parts which pass to the opposite sides of the central mass of chromosomes (Fig. 20). This is the fertilization and marks the beginning of the life of the new individual.

Before describing the next steps we must notice two important conclusions which are to be derived from the phenomena. First the facts given practically demonstrate that it must be the *chromosomes which constitute the physical basis of heredity.* The following considerations show this. It is a certain fact of heredity that the offspring may inherit equally

from each parent and hence each parent must contribute equally in the process. Now from the above description it will be seen that the egg alone (the mother) contributes cytoplasmic material, the male cell which enters the egg leaving its cytoplasm outside when it leaves its tail. On the other hand the male cell, at least in some cases, which is sufficient

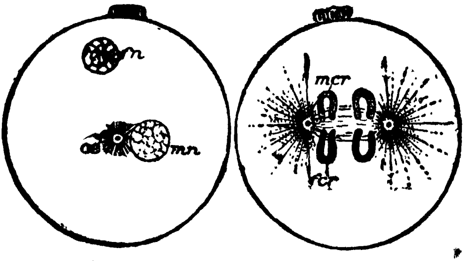


FIG. 19. FIG. 20.

FIG. 19. The chromosomes in the male and female pronucleii have resolved into a network. The male centrosome begins to show signs of activity.

FIG. 20. The centrosome has divided, and the two pronucleii have been brought together. The network in each nucleus has again resolved itself into two chromosomes which are now brought together near the centre of the egg but do not fuse; *mcr*, represents the chromosomes from the male nucleus; *fcr*, the chromosomes from the female nucleus.

for the argument, alone contributes the centrosome, the egg centrosome disappearing entirely. Hence neither the centrosome nor the cytoplasm can be the basis of heredity. On the other hand both the male and female cell contribute an equal number of chromosomes and these chromosomes are the only element contributed to the individual equally by both parents. It follows that these chromosomes must be the physical transmitters of the hereditary traits.

The second conclusion simply emphasizes the first. The egg evidently makes elaborate preparations for the reception of the male cell. At first the egg contains such a large number of chromosomes, that, if united at once with the male cell, the resulting fertilized egg would contain a number very much higher than is normal for the cells of the species of animals in question. Consequently, it throws away three quarters of this material, evidently in order to make room for the new chromosomes which are to be brought in with the male cell. The whole process teaches that the chromosomes contain the hereditary characters, and that it is a matter of such importance that their number should be kept constant that an elaborate process has been devised for the purpose of producing this result. It teaches, secondly, that there is evidently some great advantage to the organism which comes from the *union* in the fertilized egg of chromosomes from *two different individuals*. After the protrusion of the first polar cell (Fig. 17), the egg contains the proper number of chromosomes to go on with its development. But half of these are thrown away, apparently to make it possible for more to be introduced from some other source. It is especially interesting in this connection to find that eggs which develop without any fusion with a male cell, which occurs in so-called parthenogenetic eggs, only throw out one polar cell. This brings the number down to the normal and the eggs can go on developing without fertilization.

The purpose of all this is evident enough when we once conclude that the chromosomes are the

physical basis of heredity. It is seen that it brings about in the fertilized egg a mixture of hereditary material *derived from two different* sources, and this would inevitably result in *variations in the offspring.* The individual developing from this fertilized egg would tend to show congenital variations since it has resulted from the union of two different kinds of germ plasm and this fertilization may, therefore, be regarded as a method of bringing about congenital variations.

Thus far these observations are in close harmony with the theory of Weismann but they have necessitated a little change in his theory. Having found the hereditary substance, it is no longer necessary to assume that a *cell* is set apart early in the development to become the reproductive bodies, but simply that some of this *chromatic material is retained in the embryo undifferentiated*, and is eventually stored away in the ovary to become the germ plasm in the cells of the ovary. When we study the matter more closely, we find the general theory still further confirmed. According to the theory it must be assumed that some of this undifferentiated material is handed down to the next generation *without change*, while another portion begins soon to undergo a *differentiation* to produce the adult. Now this part of the theory has in a somewhat surprising manner been confirmed by observation as follows:

The fertilized egg we have traced to a point where the two lots of chromosomes come together (Fig. 20), and where the centrosome has divided, one half passing to each side of this chromatin mass.

Fibres now radiate from the centrosomes passing among the chromosomes and the latter are brought into the position of a flat plate lying between the two centrosomes (Fig. 21). Now occurs one of the most extraordinary phenomena connected with the whole process. Each of these threads of hereditary material *splits lengthwise* (Fig. 22). As we have already noticed, the only method by which a row of dissimilar bodies can be divided into two equivalent halves is by such a longitudinal splitting. If, therefore, these chromosomes represent physically the hereditary characters, it is clear that such a longitudinal splitting may divide them into two equivalent halves. If the original thread possessed the power of transmitting hereditary traits, each of these resulting halves will have the same powers. It is certainly a surprising fact to find these chromosomes, sometimes existing in large numbers, each splitting lengthwise; and it is still more interesting to find, in some cases, that the threads are actually composed of numerous beads each of which divides strictly in the middle in this splitting. But these

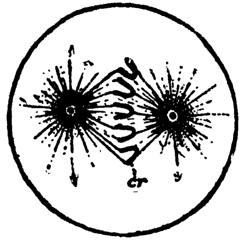


FIG. 21. The centrosomes are separate and the equatorial plate of chromosomes, *cr*, is between them.

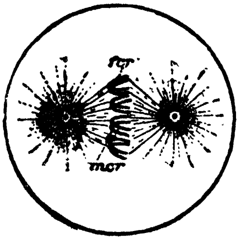


FIG. 22. An equatorial plate is formed and each chromosome has split into two halves by longitudinal division.

facts have been made out by large numbers of observations and are beyond question. In other words this chromatic material has apparently undergone a *division without differentiation.*

Now the fibers connected with the centrosomes appear to attach themselves to these threads and pull them apart. Whether this is the actual method or not, it is certainly a fact that the two halves of

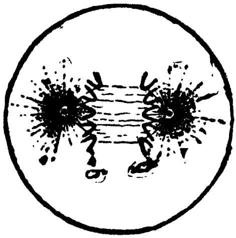

FIG. 23.

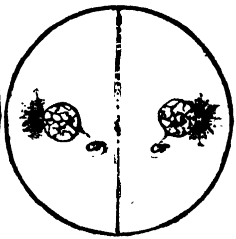

FIG. 24.

FIG. 23. Stages showing the two halves of the chromosomes separated from each other.

FIG. 24. Final stage with two nucleii in which the chromosomes have again assumed the form of a network. The centrosomes have divided preparatory to the next division, and the cell is beginning to divide.

each thread now move apart, one half of each moving toward each centrosome (Fig. 23). There is thus formed near each centrosome a mass of chromosomes and now the egg divides into two parts (Fig. 24). It is evident from this description that each of these divisions of the egg will be identical, so far as concerns chromosomes, since each contains one half of each of the original chromosomes arising by undifferentiating division. If, therefore, the original chromosomes possessed definite hereditary traits, each of the divisions of the egg will have similar

powers. It is also evident that, so long as this process continues, we may look upon the germ plasm, *i. e.*, the chromosomes, as retaining its original characters. As further divisions follow, the amount of the chromatic material increases by growth, but, so long as this same kind of undifferentiating division continues, so long will the chromosomes retain their original power of developing complete hereditary traits; so long will each cell of the dividing egg be, in matters of inheritance, equivalent to the whole egg.

But the theory of Weismann assumes that, after a little, a different kind of division arises. It assumes that, while part of the germ plasm continues to multiply in this way, another portion of it begins to undergo a differentiation to give rise to the embryo. It assumes that thus some *germ plasm* becomes separated from the *somaplasm*. This fact too has received a surprising confirmation by recent microscopic studies. It would hardly have been expected possible to find this matter demonstrable by the microscope but, apparently in some cases, traces of this new method of division can be seen. The facts upon which this statement is based are illustrated by Fig. 25. This represents an egg recently divided as above described. In the very next division, however, the two cells behave differently. The one cell, Fig. 25, *rc*, which is found subsequently to develop into the reproductive cells, and which should, therefore, receive *undifferentiated* chromosomes, divides exactly as in the first division, the two daughter cells receiving exactly equivalent chromosomes (Fig. 25, *rc*). The other cell

(Fig. 25 *bc*), which is to develop into the embryo, should, according to the theory, undergo a differentiation. Now when the chromosomes split up in this cell for division, a part of the thread is

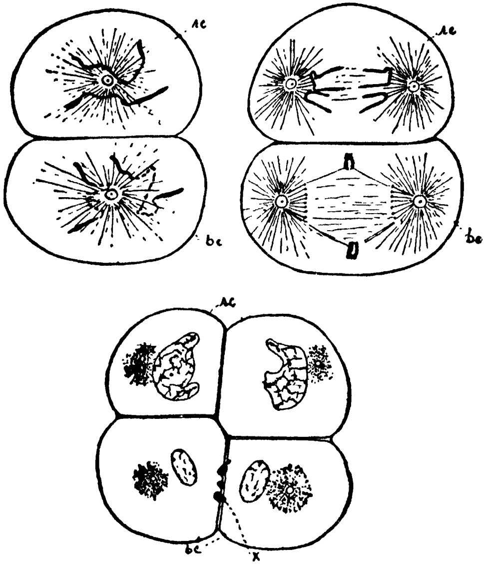


FIG. 25. Dividing egg, showing the difference in behavior of the cells which are to develop into the reproductive organs, *r, c*, from those that develop into the body, *b, c*. Extruded chromation shown at *x*. (From Boveri.)

thrown away, being extruded from the cell (Fig. 25 *x*). In this particular case the two outer ends of the threads are thrown away, only the central portions being retained. Thus the resulting cells no longer receive each a half of a longitudinally splitting thread, but only a portion of such halves. They are therefore no longer equivalent to the chromo-

somes in the original egg and not necessarily equivalent to each other. A differentiation of the germinal material has actually taken place, such that the cells which are to develop into the embryo receive some modified chromatic material (somaplasm), in distinction from the cells which are to form the reproductive bodies and continue to receive the original undifferentiated chromosomes or germ plasm. It must not be supposed that such observations as these are as yet very numerous. No one unacquainted with the obstacles surrounding such studies can realize the difficulties of making observations. But the fact that they have been found in a single case furnishes a most surprising confirmation of the notion that the real fundamental phenomenon in heredity is the transference of a definite physical substance from generation to generation, that this substance is handed from parent to child and is continuous from the reproductive organs of one generation to those of the next. In other words the explanation of heredity is to be found along the line of the doctrine of *the continuity of germ plasm.*

It is certainly a surprising fact that a theory, developed originally upon purely theoretical grounds, should find such a confirmation from observed facts. No one imagined, when the study of the egg with the modern microscope began, that it would throw such light upon the process of heredity. Weismann hardly anticipated at the outset that his doctrine would receive this sort of confirmation. The two tests of any theory are its simplicity and its ability to explain observed facts. Certainly this idea of

the continuity of germ plasm fills these two conditions so far as we have thus considered them, and it has also had the additional force of enabling the scientists to make predictions and guide in future discovery. The last-mentioned discovery of the rejection of some of the germ plasm by the cells which were to form the embryo, would hardly have attracted attention were it not for the evident significance of the phenomenon. So far as concerns such general data then, we may say that Weismann's theory has certainly received all the confirmation that could be asked.

More attention has perhaps been given to these microscopic discoveries than they seem to demand in our discussion. But the theory of Weismann is perhaps the most important addition to the discussion of evolution since Darwin. It forms an integral part of all modern attempts to discuss philosophical and social problems as well as those of evolution. For these reasons it is necessary for those who desire to keep abreast of modern thought, not only to have a clear idea of what the theory is, but also to appreciate that, unlike a large number of theories, it is something more than mere hypothesis. It makes claim to be a fact and to be substantiated by direct observation. It certainly demands consideration and, as we shall see, has demanded, in certain respects, the very general acceptance of naturalists.

### *Deductions from Weismann's Theory—Effect of Environment*

The difficulty with the theory of Weismann is not

in the theory itself, nor its lack of support, but rather in accepting some of the deductions which arise out of it. These results are in some respects so far-reaching in their consequences as to force us, if we accept the theory *in toto*, to modify our whole idea of the method of descent, and to change decidedly our conceptions of many philosophical and psychological subjects, and even to give us new notions in regard to human evolution.

In the first place, it will be seen that the theory brings into sharpest possible contrast the difference between congenital and acquired characters. A congenital character is one brought about by some peculiarity in the germ plasm; an acquired character is one produced in the body, without any relation to the germ plasm. Further, it is clear that any variation which is congenital will be almost sure to be transmitted by inheritance, since it is already in the germ plasm, while on the other hand an acquired character *cannot* be transmitted by inheritance, since it only affects the body and does not touch the germ plasm. It follows from this, of course, that the environment which acts upon the animal can produce no variations which have any influence upon the process of descent. Moreover, it is also clear that, in accordance with the theory, the environment cannot influence the germ plasm, whatever be its influence upon the body of the animal. For example, a blacksmith increases the size of his muscles by use. But the character of the arm which his child will have is determined solely by the germ plasm which this blacksmith has received at his own birth as a

legacy to the future generations. But this germ plasm is stored away in the reproductive organs, and it is difficult, indeed, well-nigh impossible, to believe that the increased size of the father's arm shall have any effect upon this germ plasm. Such at all events is the outcome of Weismann's theory. The individual is simply a product of a bit of germ plasm that is set apart to serve as a lodging-place for the rest of this precious material. The father carries the germ plasm simply as a trustee, but can contribute nothing to it nor take anything away from it. The inheritance of the race is fixed at his birth and he can do nothing to modify it. His only agency in the matter will be in selecting the character of the germ plasm which is to unite with his for the next generation, in other words in selecting his wife.

Further than this, it will follow that the effect of the environment in producing congenital variations will be nothing. Not only will acquired variations have no effect upon the germ plasm, but the environment will have no direct effect upon it. This germ plasm is inactive, plays no part in the physiology of the animal, is simply stored away in a passive condition. It is shielded from the action of the environment, just as the gold lying in the vault of the bank is shielded from the weather that beats upon the outside of the building. But unless this germ plasm can be acted upon by the environment, it follows that external conditions have nothing to do with the production of variations which influence the race. The environment may make abundant

modifications of the body of the individual, but it can produce no lasting effect, since such modifications disappear with the individual and only variations in the germ plasm are perpetuated.

Now this position is widely at variance with the attitude of science previous to Weismann. In the first place it is diametrically opposed to that which has been the general belief of mankind. The fact of heredity has always been recognized, and it has long been the well-accepted belief that animals and plants can inherit the characteristics of their parents without any special discrimination being made as to how the parent obtained the characters. Lamarck founded his whole theory of evolution upon the inheritance of acquired characters, the influence of use and disuse being the fundamental law of his doctrine. Darwin, it is true, replaced this doctrine with that of natural selection, and plainly indicated that it was his opinion that congenital characters were more likely inherited and were of much more weight in the process of descent than such effects as result from use and disuse. But Darwin carefully studied the effects of use and disuse, and came to the deliberate conclusion that they did play some part in the descent of organisms. Moreover, he regarded variations in general as largely due to the action of the environment, thus looking upon the environment as aiding in furnishing the data upon which his principle of natural selection could act. In short, while he clearly recognized a difference between these two classes of variations, he accepted both as factors in descent. Many of the students

who followed him did not see this distinction as clearly as he did, and for twenty-five years of discussion congenital and acquired characters were considered as much alike, as concerns evolution, and no attempt was made to distinguish them. Later in the discussion, as difficulties in the way of natural selection accumulated, some scientists, as we have already noticed, found a refuge again in the Lamarckian factors, since they offered variations in sufficient abundance where needed. The American Neo-Lamarckian school took up again the views of Lamarck and, with some modifications, adopted them as the primary agents in producing the origin of species. At first the dispute between this new school and the Darwinians was simply a question of degree, the new school regarding the Lamarckian factors as the primary cause of evolution and natural selection as a secondary cause, while the Darwinians regarded natural selection as the chief cause and the Lamarckian factors as secondary.

But with Weismann all this was changed. If Weismann's theory of heredity be a true one, then the Lamarckian factors can count for nothing and the Neo-Lamarckian school is entirely wrong. The environment does not affect the germ plasm and cannot therefore affect posterity. The environment cannot be called upon even to the extent of furnishing variations for natural selection to act upon. Evolution becomes simply an evolution of germ plasm and only incidentally of the individual. Natural selection acts now simply to preserve the best type of germ plasm. The individual counts

for nothing in the process except as he is the carrier of this developing germ plasm.

What factors would, therefore, be left, which could be relied upon as explaining the evolution of animals? Seemingly, nothing more than the natural selection of congenital variations. If we are obliged to exclude the environment as an agent, we must simply depend upon the fortuitous variations in the individual, which arise as the result of the mixture of two lots of germ plasm at his conception. Moreover we have not even a possibility of looking upon a uniformity of conditions as producing a constancy of variations in definite directions. So long as we could regard the environment as influencing them we could find in a constancy of conditions an explanation of the appearance of many like variations in many individuals simultaneously, and reappearing in subsequent generations. This, *i. e.*, determinate variation, we have already seen is almost necessary to an acceptance of natural selection. But with the new theory this is, of course, no longer possible. When asked for the reason for the appearance of so many variations, we have answered that the constantly changing conditions under which organisms live account for them easily enough. Species change rapidly when the environment changes rapidly, and this we have assumed is because the rapid change of environment induces corresponding variations among animals and hence furnishes material for natural selection to work upon. But with the new theory this position must be abandoned. It seems to be certain that rapid changes in environment do

produce a rapid evolution of species, but this is not because they produce variations. If such variations did come from the change in the environment, they would be simply acquired variations and could not be inherited and therefore could not count. If species change rapidly, in times of rapid climatic changes, for example, it must be due of course to natural selection. The old species have become adapted to the old conditions and so well adapted that they were kept comparatively unmodified in spite of congenital variation. During all the period of their constancy, doubtless, congenital variations, due to sexual reproduction, were constantly appearing; but the old type was better fitted to the old conditions than the new varieties, and the latter were all crowded out of existence in the struggle for life. But the moment the climate changes the old form is no longer so well adapted to the new conditions. Some of the new congenital variations would likely be better calculated to meet them and then, of course, natural selection would preserve the new varieties. The character of the whole species would rapidly change, not because the new conditions produced the variations but because they gave a better chance of life to some of the variations which had, during the period of constancy, been eliminated by natural selection.

In short, by the formulation of the new theory, the two schools came to be very sharply defined. On the one hand there is the school of Neo-Lamarckians that insists that the environment plays a part in the history of descent and that, therefore, Weismann's

theory of heredity must be false. On the other hand stands the school of the Neo-Darwinians, or Weismannians, that insists that the new theory of heredity is true and that, therefore, the Neo-Lamarckians are absolutely wrong in claiming that the environment has played any part in the evolution process other than by directing natural selection.

Weismann did not hesitate to accept the full consequences of his theory and from the very first denied the inheritance of acquired characters. To him, therefore, the process of evolution became simply the natural selection of congenital variations which have been produced by the irregular mixing of germ plasm from two different individuals. Organic evolution thus became a process of the natural selection of such variations as result from sexual reproduction. In this position Weismann soon had plenty of followers. The simplicity of the doctrine of heredity captivated science. Students of embryology soon began to find striking confirmations of the doctrine and were led rapidly to accept it. The Neo-Lamarckians had never made much of an impression upon science and therefore many scientists found little to regret in being obliged to abandon the Lamarckian factors. Further, it is evident that the new doctrine places the theory of Darwin upon an even more exalted height than Darwin himself placed it. The doctrine of natural selection had seized hold of the minds of the naturalists, and it was very easy to adopt the new view which gave this doctrine an even more prominent position. There thus arose a school of scientists who have

been called Neo-Darwinians, or Weismannians. They are, of course, followers of Darwin, but they carry his theory of natural selection to an extent further than ever Darwin pretended to do, for they make it the sole and sufficient explanation of the origin of species. It must not be forgotten that, in spite of their admiration for Darwin, they do not hold the views of Darwin, for nothing is surer than that Darwin did believe in the agency of the Lamarckian factors in the evolution of animals and plants.

### *Weismann's Theory and the Principle of Utility*

Let us now notice a little more closely the exact position which this new school of Neo-Darwinians hold as to the method of the origin of species. They can admit only the inheritance of congenital variations, and at first they regarded sexual reproduction as the sole cause of these variations, although later, as we shall see, they slightly modified this view. They must of course regard evolution as due solely to the inheritance of such variations. Now we have already seen that natural selection only touches characters which are of advantage to the individual or the race, and can therefore be used for the explanation of the origin of such characters only as are of sufficient use to the individual to have at some time determined the matter of life or death or the production of offspring. The Neo-Darwinian is therefore driven to hold that *all* specific characters are useful. Not all, however, hold exactly the same position in this respect. Wallace holds that every specific character must be useful or correlated with

useful characters, while Huxley simply claimed that each species has some distinctive specific character which is useful and which has accounted for the origin of the species by natural selection, but along with it may be others which have been associated accidentally with the useful one, but which are of no significance. But whatever view be held it is utility that furnishes the key to specific characters In order to hold this position it has been necessary, of course, to show that the principle of utility is a far more prevalent one than was previously believed. It has not been supposed in the past that most specific characters are useful, but quite the contrary. A majority of them seem to be trivial and useless. But the new theory demands utility, and as a result our naturalists have been searching industriously after possible uses of organs. Of course, just as far as they can show that this principle of utility is applicable, so far are they substantiating their claim that natural selection is the cause of the origin of species, while, if they fail, the position of the Neo-Darwinians is untenable.

Now it is certainly a fact that their success in showing the utility of seemingly useless characters has been considerably greater than would have been anticipated. The more animals and plants are studied in their natural relations, the more do the various characters appear to be of value. Seemingly useless color markings appear of value in enabling individuals to recognize each other, a matter of no little importance to them. Peculiar shapes of flowers or leaves are found to be adapted to the

visits of special insects, or to the property of properly shedding water, etc. It is not the place here to consider these details and it is sufficient for our purpose to state that the Neo-Darwinians have succeeded in finding plausible uses of organs much more widely than would have been anticipated.

Again, we notice that the new theory must find some other explanation of the seeming inherited effects of use and disuse, and it must do this on the principle of utility. The apparent effect of use is explained easily enough. For example, the monkey's hands and feet are most exceptionally adapted for climbing. The influence of use would explain this easily enough, but the new theory would discard use as effecting inheritance entirely. It would simply say that the habit of climbing trees was of great value in enabling the monkeys to escape their enemies. This being the case the monkeys that could climb the best would be the ones to survive, while the poor climbers would perish. Of course, then, if any congenital variation in the line of more effective climbing hands should appear, this variation would be selected, and, being congenital, would be transmitted to become a part of the race inheritance. Use did not produce the change or even the variations, but the variations being of all kinds indefinitely, the principle of utility simply preserved the favorable congenital variations.

Thus it is everywhere. If there is evidence that an organ is used, it follows that it is of some value to the organism, and if so it would come under the scope of natural selection. Certainly there is no

criticism of the logic of this position; the only question is as to its probability. Whether natural selection of congenital characters is sufficient to explain all characters which appear to be developed by use, is something of a question. For example, the shape of the teeth of mammals is apparently such as would have been developed by their use in grinding food. These special shapes are certainly now inherited characters. How could they have been developed? Now we can, perhaps, understand how the use of the teeth might modify their shape as they are ground over each other, and, upon the theory that the effects of use may be transmitted, we can understand how the shape of the teeth would be modified in successive generations. But it is difficult to believe that the appearance of such slight changes in shape as have appeared in the teeth could ever have been of sufficient utility to have been matters of life and death with the individuals, to say nothing of the difficulty of assuming that just such variations should have happened to appear as congenital variations entirely unconnected with use. This example is given, not as indicating a preference for the Lamarckian view, for in this case the Neo-Lamarckians have almost equal difficulty, but simply as an illustration of the sort of perplexing puzzles which are met in trying to apply consistently the principle of natural selection of useful variations.

### *Weismann's Theory and the Principle of Disuse—Panmixia*

A graver difficulty appears in the attempt to explain what appears to be the disappearance of organs

through disuse. It may be possible to believe that an organ which is used may increase by the action of natural selection, preserving in successive generations the most efficient variations. But it is not possible to explain the disappearance of organs through disuse in the same way. For example: some cave animals have no eyes, and we could easily understand their loss if acquired characters were inherited. To animals living in dark caves eyes are of no use. But in order to suppose that they are lost by natural selection we should be obliged to assume that the individuals with poor eyes were *better* equipped for the struggle for existence than those with good eyes. Only under these conditions could the principle of survival of the fittest preserve the successive grades of imperfect eyes. Natural selection could not preserve the eyeless individuals at the expense of the others unless they were for this reason actually *better* equipped for the struggle for existence.

This difficulty is met by Weismann with an appeal to a new principle, which is essentially the result of the *withdrawal* of the action of natural selection. We can, perhaps, best understand this principle by an example. For this purpose we take the Irish potato, a species of plant which has been developed under cultivation, and which is therefore better understood than any wild variety. By the high cultivation to which the potato has been subjected by the agriculturalist, its tubers have been greatly increased in size until they have become very different from the original tubers of the potato

plant. This increase in size has been produced, partly by the selection of the largest tubers for seed purposes, and partly by the high state of cultivation to which they have been subjected. Now nothing is more certain than that, if the potatoes should be left alone to grow wild under the conditions of nature, this large-sized tuber would disappear in a comparatively short time. Perhaps it might not be reduced to a size quite so small as that of the original potato plant, but certainly the large-sized tuber of cultivation would be soon reduced in size. The explanation is very simple. This large tuber has been produced by selection of the largest tubers for breeding and by high cultivation, and, as long as these conditions remain, so long will the tuber retain its newly developed characters. But these conditions are retained only by a constant selection of the best varieties. Every farmer knows that he gets the best crops by using the largest tubers for seed; in other words, the new variety is *preserved* by a constant selection of the best plants. Let the farmer withdraw this selecting influence and use all sorts of tubers indiscriminately, small as well as large, and the result would be, in a comparatively few generations, a great reduction in the size and value of the tuber. In other words, even after the large-sized tubers have been produced by selection there is still needed the same sort of selection to preserve them. Here is a principle that every farmer and every breeder of animals recognizes. If left to themselves for all varieties to breed together, the highly developed forms of our cultivated animals and plants

soon disappear. This fact has, indeed, been frequently used as an argument against the belief in evolution.

Now this same principle is applied by Weismann to explain the apparent reduction of organs by disuse. A character which has been developed by selection can remain only as long as the selection preserves it; but just as soon as the conditions change and selection no longer protects the character in question, it will tend to disappear, just as would the large potatoes. For example, eyes have been developed by a long-continued operation of the law of natural selection. They are adaptive organs and their development has been brought about by the rigid exclusion of the individuals with inferior powers of vision. But, just as in the case of the potato, after this organ is developed its preservation requires the same exercise of selection. If all kinds of eyes, good and bad, had an equal chance to be preserved, the eye would begin to degenerate. But the selection of the eye can only take place in light. If, therefore, the animals live and breed in dark caves, all of the influence of selection will be withdrawn, and the animals, so far as concerns their eyes, will undergo the same sort of history as would the potato if turned out wild to care for itself. Their eyes would begin to lose their efficiency, not from *disuse*, but simply because all sorts of good- and bad-eyed individuals breed together, and nothing would preserve the efficient eyes at the expense of the poor ones. In other words, natural selection is needed to *preserve* an

organ just as truly as to *produce* it. Moreover, in this particular case it is urged that in the cave the animals with well-developed eyes would actually be at a disadvantage. Their eyes being of no use would be constantly exposed to injury from running into objects in the dark. On the other hand, the animals that had highly developed organs of touch or smell would possess a great advantage over those with well-developed eyes. Hence natural selection would be directed toward developing organs of touch instead of retaining and developing eyes. If, moreover, the delicate eyes were a source of trouble, from being constantly exposed to injury, natural selection would begin actually to eliminate the individuals with sensitive eyes and retain those with the sense of touch and smell well developed. This would, of course, lead to the reduction and disappearance of eyes. It would thus happen that results would arise that seemed to be due to disuse, but were really due to selection.

This principle Weismann called *panmixia*. It evidently consists in the withdrawal of the action of natural selection in regard to some characters, and the consequent perfectly free interbreeding of individuals without any reference to the character in question. The law is a very general one and has wide application.

Panmixia is the principle called upon to explain the loss of organs or their degradation to a rudiment. But while it will account for the degradation in the size and efficiency of organs which are no longer of value, it does not account for their complete

disappearance. Even Weismann admits that panmixia is not wholly sufficient. Now there are many illustrations of the complete disappearance of organs, as for example the loss of legs in the snakes, and inasmuch as panmixia does not account for such instances, we cannot look upon it as a sufficient explanation of the apparent loss of organs by disuse. The application of this principle of panmixia to man is one of great importance.

Thus it is that the formulation of Weismann's theory of heredity has led to Neo-Darwinism. This theory is bound to find all specific characters useful or correlated with useful characters. It must explain all seeming effects of use and disuse either by natural selection or by the withdrawal of selection in the case of non-useful characters. It must deny that the environment has any directive influence upon the appearance of variations, and deny, therefore, that it has any direct influence upon evolution. It must find the explanation of all the phenomena of descent in the selection of congenital characters, produced, perhaps, primarily by sexual union.

### *Weismannism as Relates to Human Progress*

We can have a better appreciation of the interest which surrounds the discussion of Weismannism if we notice certain other deductions from the theory. If this theory were simply a theory of heredity it would have been like other theories, interesting enough, but scarcely one to attract attention outside

of biological science. But it is much more than a simple theory of heredity, since it involves the whole law of progress.

Entirely independent of its interest from a zoological standpoint, the subject, especially as concerns the non-inheritance of acquired characters, has very close relation to many problems of human development. It has certainly always been a belief that conditions surrounding the parents have some influence upon inheritance. Holmes has tersely expressed that belief in the oft-quoted expression that a child's education ought to begin one hundred years before he is born. By this is, of course, meant that, in order to produce a child with proper inherited characters, his parents must begin training for it and even his grandparents, and, unless they live the proper kind of life and become properly educated, the inheritance of the child will suffer. But plainly in accordance with Weismannism, this does not follow at all. Such an education of the ancestors would simply produce in them certain acquired characters and, since these are not inherited, this previous training would not in the least affect the child, except so far as it might cause the parents to lead a different kind of life and make them likely to give the child a better education. The child's education begins only *after* he is born, and the education of his parents has no effect upon the characters which they transmit to their offspring. There is a widespread belief that a drunkard's appetite is transmitted from father to son. In certain respects this is doubtless true. Beyond a doubt the children of

a drunkard are in danger of inheriting an appetite for alcoholic drink. From this aspect of the question many a moral lesson has been drawn, that, by indulging in this appetite, a man is entailing the same appetite upon his offspring. We have taught that if a man acquires an appetite for alcohol he is likely to transmit that appetite to his later-born children. But this again is a mistake, if this new theory of heredity is correct. An acquired appetite is an acquired character and cannot be transmitted by heredity. If this man did not himself inherit the appetite, the fact that he developed such an appetite by the use of alcohol would not in the slightest degree affect the traits which he transmits to his child. Of course a child born in a drunkard's home, surrounded by saloons, and with parents setting him the example, will be quite likely to acquire the appetite on his own account; but if the father, instead of *inheriting*, *acquired* the appetite it cannot be transmitted to the son. On the other hand, if the father should himself inherit the appetite but should never indulge that appetite during his life, this would not prevent him from transmitting the same appetite to his child. In other words, the sort of life the father leads does not in the slightest degree affect the characters which he transmits to his son. It is evident that such a conception will greatly modify our ideas of morality.

The same principle is of very wide application, for, in accordance with this idea of heredity, nothing that the individual may do during his life will affect the offspring, so far as inheritance is concerned.

Whatever be the life that the parents lead, whether of the most ennobling or the most debasing character, this will not modify the characters which the offspring would receive. Of course the life of the parent has a very great influence upon the child by the way of education and imitation, but, if the new theory of heredity is correct, it will be *only* by imitation and education and not by inheritance. Imagine two individuals with the same congenital characters, and suppose that one is placed in circumstances which lead him to the lowest stages of dissipation, while the other is surrounded by conditions which lead him to live a most upright, moral life; imagine that each has a son who is separated at once from his parent and brought up under identical conditions; it would follow that each of the boys would show the same inherited characters. The profligate life of the one parent and the upright life of the other would not count in inheritance. Such a position is, at all events, somewhat revolutionary.

From such considerations it would follow that the only control that a man has over the inheritance of his children is in selecting his wife. If only modifications of the germ plasm can count in inheritance, and if these modifications come wholly from the mixture of two bits of germ plasm in sexual reproduction, then it follows that the only method by which a person can influence the inheritance of his children is by choosing the character of the germ plasm which combines with his own to form the next generation. He may have a profound influence

upon his children by means of the environment with which he surrounds them and the education he gives them. But upon the characters which they inherit his power ceases after he chooses his wife. Such considerations of course even more highly exalt the great significance of marriage, and bring the importance of choice of a husband or wife into even clearer light. If the wrong mate be chosen no subsequent education can correct the evil which is stamped upon the offspring.

It is clear that these conclusions very decidedly modify many current notions of development, and change our ideas of responsibilities. It changes the attitude of the individual toward his ancestry as well as his posterity. He cannot transmit bad acquired habits to his child, and, on the other hand, he cannot lay his own shortcomings upon the bad habits of his parents. But it would lead to some disquieting conclusions as well. It would indicate that by no possible moral method of living could a person eradicate from his race certain evil congenital traits which he may have inherited. Moreover, if variations are all congenital and due to some little-understood mixing of germ plasms, nothing that the individual can do will make it sure that his children may not suddenly start a new line of evil inheritance. Congenital variations we cannot control, and no upright life can therefore protect posterity with any certainty. The great significance of such conclusions will be readily seen without further emphasis.

In still another line do we see this theory resulting

in somewhat surprising conclusions. If we compare man of the nineteenth century with man of one thousand years before Christ, we find a striking contrast. Civilization has been advancing very rapidly and making great conquests. The man of to-day rises very much higher in the scale of accomplishment and power than the man of an earlier date. As we study the history of civilization it seems to be manifest that man has been steadily advancing and that mankind of to-day is vastly superior to mankind of three thousand years ago. Moreover, we have always tacitly assumed that it is civilization that is raising man and that, as his knowledge and education increases, they are lifting him into a higher plain of development. Is it possible to remember the wonderful attainments of man to-day and compare them with those of the most exalted men of earlier days, without believing that man of to-day is superior to the man of old? Or look at the matter in another way, and compare civilized man with the savage. Even the lowest members of civilized communities are, so far as concerns possibilities of achievement, far ahead of the most intelligent representatives of the savage tribe. Can we compare Lincoln with Sitting Bull without feeling that Lincoln is infinitely ahead of the Indian? Or compare Beethoven with a musician of a savage tribe who finds the height of his musical nature satisfied by the beating of a tom-tom or by the few squeaky notes of a rude wind instrument. Can we doubt that Beethoven has the greater musical nature? In other words, is it not clear that civilization *has*

elevated man, and that under its influence we are slowly but surely gaining, not only greater intelligence, but greater mental attributes?

But here, too, we find that the new theory demands a complete modification of our views. Civilization and education are external and not internal, extrinsic and not intrinsic forces. It has changed the environment in which man lives. It has wonderfully changed the education which he receives and the tools which he has at his command. It has changed the opportunities which are presented to him. It has given him a new vantage ground for action, since it has increased his knowledge of nature. Civilization has changed his surroundings, but has it changed *the man?* To-day he is put into possession of all the information which has been accumulating by slow steps for the last two thousand years. He learns in a few months how the forces of nature have been mastered. He learns facts which took centuries of slow discovery to bring within the reach of man. The art of printing gives him in a few years all that millions of men have spent their lives in laboriously discovering. Civilization and advancing knowledge put into his hands new facts, new forces, new laws, new methods, new tools of every sort. Doubtless Lincoln was vastly superior to Sitting Bull. But Lincoln had a much superior set of tools to work with. He had a nation of millions of thinkers to assist him. He had the whole experience of the last two thousand years to guide him. He had great problems forced upon him and he was forced to solve them because he

lived in contact with a vast nation of men. Sitting Bull, on the other hand, had a handful of men behind him. These men were without education and knew nothing of what earlier generations had learned. He had no experience of a thousand years to guide him. He had no history to serve as a finger-post. He had no literature and only a few traditions to spur him on. He did not have at his command the accumulated information of science for centuries. He was obliged to begin at the beginning and learn everything for himself. Methods and principles alike must he learn, and in the learning he had only a few crude traditions as a guide. Of course Sitting Bull was inferior to Lincoln. But if you could have given Sitting Bull the advantage of Lincoln and had required Lincoln to grow up in a savage community with only a savage education, who would venture to say that the intelligence of the Indian would not have shown forth as the statesman, while Lincoln would have been simply a savage chief ? Was not the difference between them one of tools and opportunity rather than one of actual mental power ?

Beethoven doubtless developed music to a much higher plane than it has ever been developed in the hands of the musician of a savage tribe. But it must be remembered that Beethoven found music already highly developed. The savage has no instruments except the tom-tom and the squeaky flute, while Beethoven had the piano and the orchestra. If Beethoven had found only the tom-tom and the flute at his command we should have had no symphonies from his genius. If he had been

born a savage, even admitting that his musical talent was equally great with that which he had as a child of civilization, it would have expended itself in beating the tom-tom and playing the flute. Perhaps it might have resulted in the invention of a new musical instrument for his tribe, but this must have been the limit. On the other hand, if the savage musician, who, even with the tom-tom and the flute, contrives to obtain some music, had been brought into a civilized community, taught the facts which Beethoven was taught, taught to play the piano and given fundamental principles of music as an education, who would venture to say that he might not have developed a symphony? He uses the instruments he has to their highest extent. Beethoven with better tools and better education accomplished more.

In short, the question is forced upon us whether, in spite of his greater achievements, mankind is provided with any greater natural powers than in earlier centuries. This conclusion, it is seen, follows in reality out of Weismann's theory of heredity. Civilization is something external to man's nature. Education is an effect produced upon man's body, but not on the germ plasm. All of the phenomena of civilization have been developed by the powers of body and brain and the germ plasm has nothing to do with it. Now, if acquired characters are not inherited, it plainly makes no difference how many generations you educate the race or how many generations of musicians follow one another. These influences would not affect inheritance, for they

would all be simply *acquired attainments*. Of course, it might be that the mental powers of man have developed parallel to this advancing civilization, developing as the result of the preservation of congenital variations. But this would be *independent* of civilization and not *because* of it. In accordance with the new theory of heredity, it would be impossible to produce variations in the germ plasm which would give rise to larger brain power by simply training the brain of the individual who is carrying this germ plasm as a trustee for future generations. Nor would it make any difference whether you educated his brain for a single generation or for a thousand generations. If acquired characters are not inherited, no amount of education could by any possible means affect the brain power of the offspring. If, therefore, the brain power of man has developed during the growth of civilization this has been due to natural selection and not to the direct effect of civilization or education.

Such at all events is the position which the Weismann school adopt, and they bring forward various lines of evidence to show that this conclusion is really in accordance with the facts. They insist that everything points to the conclusion that the Greek of Athens was intellectually the equal of the Caucasian of to-day, even in his highest state of development. They insist that when we compare the Greek with the modern man along lines in which they had equal facilities, the Grecian does not fall behind the European. Of course, when we come to subjects where the accumulated knowledge of the

race can have its influence, the man of to-day is vastly the superior, since he has a better vantage ground. But Grecian art demanded no special knowledge of science, and it has not been surpassed even in later days, while Grecian literature still stands among the world's masterpieces. In the fifteenth century man invented printing, and the wonderful growth of civilization has been a consequence. But while printing has most marvellously increased the amount of information with which a man can begin the active life that follows his early education, there is no reason for thinking that this in the slightest increases his innate powers. Because of the knowledge of printing we are better informed, we have better tools to work with, and our lives can begin where our ancestors left off, but is there any reason for believing that we have any greater brain power than our ancestors of two thousand years ago? Of course the Weismannian school does not deny that there may be such a thing as increase in mental power. Such has doubtless occurred in the passage from animal intelligence to that of man and it may still be going on. Civilized races may have a higher innate power than savages. But, if this is so, the growth of mental power has *not* been brought about by the exercise of the powers which we have, nor has it been produced by civilization itself, since these are acquired characters. It has been produced simply by the selection of the best congenital variations. Civilization and education are wholly extrinsic forces and have no relation to the intrinsic development of innate attributes.

Such conclusions, of course, show human history in a new aspect. If this conception be true the study of civilization is not the study of evolution at all. Mankind has been developing by the slow accumulation of innate characters due to variations in the germ plasm. That is his real development. But entirely apart from this he has learned the art of recording the achievements of the past in such a way that future generations may profit by them without the trouble of discovering them. These acquired powers have accumulated age after age and constitute civilization, but they do not represent human development.

### *Summary*

The past century has seen many theories advanced which try to explain heredity, but the only one that has made any impression upon science is that suggested by Weismann in 1883. This theory, because of its simplicity, received from the outset a wide support and, later, it has received surprising confirmation from observation. The theory of the Continuity of Germ Plasm consists essentially in the supposition that the basis of heredity is a material substance which is handed down from generation to generation and which is named *germ plasm*. This material is carried from age to age in the reproductive organs of the individual. The individual is only the result of the unfolding of the potential powers of a bit of this germ plasm and, once developed, he carries the rest of this precious material around with him to

hand it down eventually to his offspring. While in the individual the germ plasm increases in amount, but he cannot change its character. It is intrusted to his keeping, but no peculiarities which he may develop can affect it, and hence acquired characters cannot be transmitted to his offspring. To avoid the constancy which would result from such a condition of things sexual reproduction has arisen among organisms, as the result of which two bits of germ plasms from different sources unite in the reproductive act. Their mixture produces variations in the germ plasm and hence the offspring shows congenital variations which are in turn transmitted by heredity. But the environment of the individual, since it affects the body but not the germ plasm, cannot affect inheritance, and hence plays no direct part in evolution.

With this conception evolution becomes simply the natural selection of such congenital variations as best adapt the individual to the surroundings. Natural selection simply picks out the most favorable varieties of germ plasm, causing the destruction of all less favored kinds. This of course makes it impossible to admit that use and disuse and the [illegible]ronment generally have anything to do directly [illegible]. It makes utility the one agency in determin[illegible], and forces upon us the claim that *all* specific characters are useful. It finds an explanation of the loss of such organs as are of no use by the principle of panmixia, which simply means that natural selection is required to preserve an organ in an active condition as well as to

produce it, and if this action is withdrawn the organs will degenerate from promiscuous breeding. Lastly, it is seen that this theory has especial effect upon our conception of human evolution, forcing us to assume that man, so far as concerns his innate characters, is not advancing by civilization and education, and thus requiring a very considerable modification of our previous conception of man's relation to education and moral responsibilities.

These very far-reaching deductions make Weismann's theory of heredity one of the most suggestive contributions to science in recent years, and demand a more thorough understanding of it and its effects upon the doctrine of evolution. To this further consideration we now proceed.

# CHAPTER VI

## METHOD OF EVOLUTION UNDER THE LIGHT OF WEISMANNISM

IT is clear that the problem of the method of evolution assumed a new aspect under the influence of Weismann's theory of heredity. If we accept the theory as above outlined it would require us to change our notions of the method of descent very profoundly. It would be necessary to remodel them in such a way as to leave the preservation of congenital characters alone as the cause of all phenomena connected with the origin of species, and natural selection would appear, at first at all events, to be the only force capable of directing the selection of those congenital variations. The followers of Weismann have not hesitated to take this position and insist that natural selection is sufficient for all purposes, thus giving rise, as already noticed, to Neo-Darwinism or Weismannism. These two terms, so far as concerns the theory of the method of evolution, have essentially the same meaning. We will hereafter use the term Weismannism, since this expression conveys a little more accurately the

conception of evolution as produced wholly by the selection of congenital variations.

The law of natural selection, as we have seen, even before Weismann, had been quite severely criticized, and many naturalists, including Darwin, had become convinced that it was not quite so all-powerful as at first imagined. But with Weismann natural selection received a new foothold and, in a few years, came even more prominently to the front than ever, since it was more sharply contrasted with other theories. In Darwin's hands natural selection received aid from use and disuse, from the direct effect of the environment in causing variations which could be selected, in the direct effect of the inheritance of acquired habits, etc., and all these forces were supposed to act together. In Weismann's hands natural selection is deprived of all these secondary aids and stands alone.

At first the attractiveness of the new theory led to a temporary forgetfulness of the objections raised against natural selection. But these soon came up again with redoubled force, since with Weismann everything must depend upon the one powerful law. Some of the questions which have arisen in connection with the sufficiency of natural selection we have already considered in a previous chapter, where we saw that they gave rise to a demand for a further study of the cause and nature of variation. Having now seen one answer given in recent years to the question of the origin of variations, viz., a sexual union of different germ plasms, we return again to consider the theory of natural selection somewhat

more searchingly. In the following review of the obstacles in the way of natural selection we must constantly bear in mind that they are not objections to natural selection as a law in nature, and not to Darwin's conception of that law. The criticisms are forcible only against the new aspect which the doctrine has been forced to assume by Weismann's theory of heredity. It is only when the doctrine of natural selection is claimed to be a complete explanation of the method of the origin of species that criticisms as to its inadequacy in some respects become of any significance. One can admit the force of all these criticisms and still accept Darwin's views, but he cannot admit them and accept the belief of the Weismannian school.

### *Relation of Weismannism to the Problems of Variation and Evolution*

We notice first that a considerable number of criticisms are simply the result of misunderstandings, and upon these we need not dwell. Among them may be mentioned the claim that natural selection personifies nature; the claim that it offers nothing in nature to replace the selective action of the breeder in mating together individuals with desired characters; the claim that all species ought to *advance* as the result of the law, while it is well known that some have remained stationary for no one knows how many thousands of years; the claim that we never ought to find inferior species in existence, since the better ones should take their place.

These matters need not detain us, since they are simply the result of misconceptions of the meaning of natural selection, and vanish as soon as it is understood.

There are, however, other difficulties of more weight. First may be mentioned again the problem of utility. We need only say that to Weismannism all characters must be of sufficient utility to have determined the matter of life or death or the production of offspring, or must at all events be correlated with such organs. It is doubtless difficult to conceive that all of the seemingly insignificant characters of species, which are nevertheless of specific value, have ever determined the survival of the lines of descent of such animals as possessed them, amid the extermination, with failure to perpetuate their line, of such individuals as failed to possess them. In spite of the fact that naturalists are more convinced than in earlier years that an extremely small variation may be of use, and of sufficient use to determine at least the matter of fertility, as illustrated in a previous chapter, it can hardly be claimed, considering the demonstrable uselessness of some characters, that Weismannians have substantiated the fundamental position that *all* specific characters have been developed through the law of utility.

Again, reference must be made to elimination by cross-breeding. As we have seen, the breeding of individuals possessing favorable variations with those not possessing them will be sure to eliminate a new character if it occur only in a single individual, and

this has led to the general recognition that individual characters can count for little in the process of evolution. To be preserved amid promiscuous cross-breeding a variation must occur in many individuals at once. Now Weismannism utterly fails to explain how many individuals can vary simultaneously in the same direction. Variations always come from the mixture of germ plasms in sexual reproduction, and it is impossible that the same mixture should occur in the offspring of any two pairs of individuals. We can therefore see no reason why congenital variations should occur in many individuals at once in the same direction. Thus natural selection would be forced to act solely upon the principle of means and averages, a principle satisfactory enough in explaining the development of organs in size and efficiency, but in other places, especially in explaining the beginning of organs, quite inadequate.

Has the theory of Weismann answered the question of the beginnings of organs, which we have seen is involved in the problem of the origin of variations? It has at all events offered a suggestion. Weismann furnishes an explanation for the origin of variations, finding it in the mixture of two bits of highly complex germ plasm at the time of sexual reproduction. We can easily see how this may explain the origin of variations, and how it may even account for what we have called discontinuous variations. But such variations would be purely hap-hazard, occurring in no definite direction and only in single individuals at once, and would of course have no relation to the needs of the individual. If an animal were placed

under conditions where a long neck was needed, there would be no more reason for expecting, among the congenital variations, animals with long necks than animals with extra toes, or with short legs, or with changes in the color of the hair, or any other miscellaneous character. In such an example there is perhaps no real difficulty, for it is easy to see that the animals will be born with necks of varying length. We may simply suppose that natural selection exterminates the short-necked individuals, while the variations in number of toes, color, etc., not affecting the problem of getting food, would not be touched by selection, and would come and go without leaving permanent effect. But a real difficulty comes when we consider structures which could not have been produced by the accumulation of slight increments since they require the adaptation of different parts together, as, for example, the heavy antlers and massive shoulders of the deer. The best illustration of this subject occurs among instincts which will be noticed a little later.

Again it must be noticed that, while Weismannism accounts for variation, it utterly fails to account for determinate variation. As we have noticed, our paleontologists, who have studied evolution over long ages of the world's history, have become convinced that variations have not been fortuitous, but along certain definite lines. Such a conclusion is certainly at variance with the theory of Weismann. The origin of variations from mixtures of germ plasm offers no opportunity for determinate variation. Now it has not been positively demonstrated

that such determinate variation is a fact of nature. If it could be positively proved it would be fatal to the view that finds the cause of evolution to be natural selection of fortuitous variations. But the evidence for the occurrence of variations along definite lines is of such a character as to have convinced paleontologists of it, and in the last few years the belief in such a law has been growing. Even Weismann in his most recent publications has felt the necessity of explaining the matter. He has recognized that variations not only seem to appear in definite lines, but that they appear where they are needed, two facts utterly at variance with the Weismann theory, so far as we have considered it up to this point. If, then, we find Weismann admitting that variations are not hap-hazard, as they would necessarily be, according to the explanation which he gave them at first, we may feel pretty well assured that the evidence of such determinate variation is so strong that the fact must be included in any satisfactory theory of descent.

Beyond question it would aid considerably in the solution of some of these difficulties, especially that of determinate variation, if we could believe in the inheritance of acquired variations, as Darwin did, even to a slight extent. If such an inheritance does occur in any degree, it will be a directive force, and will determine the direction of variations which may subsequently be preserved. It would thus in the end be a most powerful force. But Weismann's theory of heredity deprives us of its aid. It can probably be stated without danger of dispute that,

with the exception of a few extremists, naturalists generally recognize the great weight of the difficulties, and realize the serious obstacles in the way of accepting natural selection as a sufficient cause for organic descent, as we must do if we admit Weismann's theory of heredity. But this does not mean that we must give up either natural selection or the new theory of heredity, but simply that natural selection of accidental variations which come from mixtures of germ plasms is not alone sufficient to account for descent. The actual condition of the discussion was excellently expressed by Osborn when he said: "If acquired variations are transmitted there must be some unknown principle of heredity; if they are not transmitted, there must be some unknown factor of evolution." This statement was originally made by one of the opponents of the Weismannian school, but it has lately been quoted with approbation by Weismann himself as expressing the present condition of the discussion. Since, then, it represents the position of the two opposing schools, we may regard it as representing a quite general opinion of science to-day.

It will be evident by this time that the new theory of heredity is something more than a simple hypothesis as to the process by which heredity takes place. Its results extend in every direction in philosophy and science. It involves the whole conception of the method of evolution, and, if it be true, it involves fundamentally new ideas. With all this in its train it is easy to understand the intensity of interest that has centred around this seemingly in-

nocent attempt to explain the process of heredity. It is easy to understand how the discussion of this theory has been the active topic of debate in the last fifteen years. Since Weismann propounded his theory there has hardly been a gathering of scientists that has not brought forth a consideration of this or kindred topics. The extreme significance of the theory, if true, offers a sufficient excuse for the study of such an obscure substance as *germ plasm*, a substance which is of course purely hypothetical.

This brings us finally to the question of fact. Is it a fact that acquired characters are not inherited, or is this simply a mistaken deduction from an undemonstrated hypothesis ? Up to this point we have considered Weismannism simply as a theory. Now we must ask how it coincides with facts. If Weismann's theory be true, is it so strictly true that the inheritance of acquired characters must be positively denied, or may it be so modified as to admit of such a possibility ? Which of the horns of the above dilemma must we seize ? Is there an unknown factor in heredity that makes such inheritance of acquired characters possible, or is there some unknown factor of evolution which explains the phenomenon of descent without such inheritance ?

### *Weismannism both a Theory of Heredity and a Theory of Evolution*

In trying to determine whether Weismann's theory of heredity coincides with facts, we must first notice that there are two entirely different sets

of facts which the theory tries to explain. First we have the facts of heredity itself. Ostensibly it is the sole purpose of the theory of the continuity of germ plasm to furnish an intelligible explanation of the fact that the child resembles its parents. The second fact is that of evolution. Weismannism is not simply a theory of heredity, it becomes at once a theory of evolution. It explains heredity by the continuity of germ plasm, but it explains evolution by the natural selection of congenital variations which have resulted from sexual union. Of course these two sides of the theory are closely connected, the second being clearly derived from the first. But they are nevertheless two distinct problems. The theory of heredity might be true, to a large extent at least, and yet the application to the problem of descent be false. It may be true that the continuity of germ plasm is the basis of heredity, but that some other force than sexual union with selection has also been at work to produce organic evolution. Some such position as this we shall presently learn is held by probably a majority of scientists to-day.

If the theory were simply that the basis of heredity is a germ substance, which is handed down from generation to generation, from parent to child, through the reproductive cells, and which is carried from generation to generation, only increasing in amount meantime, it is likely that there would be little dispute over it. Such a conception is at once so simple and so completely in accordance with facts that it carries great weight in itself. But Weismann added two other items to this conception, which

made it much more than a simple theory of heredity. In the first place he has assumed that this germ plasm is *absolutely stable*, *i. e.*, not itself subject to change under the influence of the environment. The body of an organism is certainly subject to very great changes produced upon it by the environment. In contradistinction to this the germ plasm is assumed to be absolutely stable. It is said to be handed from parent to child, and then passed on by the child *exactly* as he received it. Although it may increase in amount as the reproductive organs grow, it remains unmodified, no matter what be the change in the conditions to which the individual is subjected. The germ plasm is said to be absolutely constant except as union with other germ plasm produced variations.

Second, Weismann assumed that this germ plasm is *perpetually continuous*. By this is meant that the germ plasm is always handed down from parent to child without any possibility of the body of any individual contributing anything to it or taking anything away from it. There is no possibility of commerce between the body and the germ plasm. These two conceptions, that the germ plasm cannot be modified by environment and that it can receive no contributions from the body, constituted essential features of Weismannism in its original form. Upon the first conception, that of stability, was based the theory of development by sexual union, and upon the second, that of continuity, was based the denial of the inheritance of acquired characters. If either of these conceptions be abandoned, evidently

the Weismannian theory of evolution must be modified. We shall see that both positions have been virtually given up.

### *Stability of Germ Plasm—Theoretical Conclusions*

It is this phase of the theory that has made necessary the claim that all variations which count in evolution, *i. e.*, all congenital variations, have come from mixtures of germ plasm. In other words, it is this idea of absolute stability that finds in sexual union the sole cause of congenital variation. Any modification of the germ plasm would result in a congenital variation. All congenital variations are factors in evolution, and hence any force which modifies the germ plasm is a force in evolution. If, however, the germ plasm is absolutely stable, then congenital variations can only come from mixtures of the elements already in this plasm.

Now logically there is no reason why we may not conceive other methods of producing modifications in the germ plasm. Its absolute stability does not need to be a part of the hereditary theory, and, moreover, this idea of stability receives no confirmation. It is just as simple to conceive that the germ plasm is subject to variations as to assume that it is absolutely stable. We may easily suppose that it is subject to internal spontaneous variation owing to its instability, or that the conditions around it have direct influence upon it. It may easily be that, owing to an insufficiency of food supply, the animal or plant that carries a given bit of germ plasm is

poorly nourished. If this be the case it is natural to suppose that the germinal material would be directly affected. Or, again, we might suppose that some acquired variation in the individual, produced by use or otherwise, would so affect the body of the animal as to produce profound physiological disturbances which would put the germ plasm under new conditions. If this should occur it is natural to suppose, provided we do not assume by theory that the germ plasm is absolutely stable, that it would be modified by the new conditions. It must be noticed that this does not by any means imply the inheritance of acquired characters. Very likely there will be no similarity between the modification which has occurred in the body as an acquired variation and the variation in the germ plasm which results from it. The individual may, for example, lose an eye by disuse, and this might so affect its physiology that the germ plasm would be modified by the new conditions and the next generations would show variations, not indeed in the direction of diminished eyes, but in some indefinite way. The variations of the next generation would be haphazard so far as concerns any relation to diminished eyes is concerned. It would be no more likely to have diminished eyes than increased eyes, or, indeed, variations in an entirely different direction. Thus there would be really no inheritance of acquired characters. The fact would be simply that a change in the environment produced acquired variations in the body of the individual. The new variation thus produced threw the body out of adjustment, and the

new physiological conditions placed the germ plasm in new conditions, causing it to begin to vary. The changes in the germ plasm would produce congenital variations in the next generation, but they would be without any direct relation to the acquired variation developed in the last generation.

Now this conception is just as plausible as that of absolute stability. There is nothing in the nature of germ plasm to indicate that it must be stable unless we voluntarily imagine it to be so. On the contrary, since it is the most complex substance of which we have any knowledge, it would be most likely to be very unstable. It is well known that simple bodies are commonly stable, while complex ones are unstable. Certainly germ plasm, if such a substance exists, containing as it does the characters of the adult in small compass, must be inconceivably complex. Why then should we be asked to believe that it is the most stable of all organic compounds? Logically, therefore, without any reference to the matter of the inheritance of acquired characters, it would seem more likely that this substance would not be stable.

Nor does such a position mean the rejection of the new theory which finds in the continuity of germ plasm the explanation of heredity. The study of the egg shows us that some sort of hereditary substance is handed from parent to child, and is then probably set aside to form the hereditary substance of the next generation. There is nothing in this conception to lead us to deny that this germinal substance may be subject to change with changed

conditions. The reason why it was supposed to be so stable was largely because it was assumed that this substance was stored away in the reproductive organs, far from any opportunity of being influenced by the environment. But even here it would perhaps be affected by physiological changes in the individual, and, moreover, as we shall see, it is now admitted by Weismann that his germ plasm may be more or less widely distributed through the body instead of being confined to the reproductive organs. Nothing, in short, indicates that this material is out of reach of the environment. All that is really suggestive in the theory, and all that receives confirmation by observation is retained, even if we do admit that this germ plasm is not absolutely stable but is subject to variations. If such variations occur they would, of course, have an effect upon evolution, since they would necessarily be inherited. This conception is not the inheritance of acquired characters, but simply the independent variability of the germ plasm.

So thoroughly convinced have some naturalists become of the instability of this germ plasm that they have actually reversed the theoretical conclusions of Weismann. Germ plasm, being the *most complex* of bodies, is said to be also the *most unstable.* Instead of remaining constant generation after generation, as Weismann supposes, it is said that it is constantly changing, *never* remaining stable. The child can never be like its parents because of the constant variability in this substance. Sexual union has therefore exactly the reverse

effect from that supposed by Weismann. The offspring of sexual union, instead of being more variable than the parents, is half way between them, and hence departs *less* widely from the mean than its parents. Sexual union thus tends to *prevent* wide variation rather than produce it, and is thus the force which holds in check the universal tendency of germ plasm to vary. This position is manifestly exactly contradictory to that of Weismann in almost every particular where it affects the problem of evolution. This view of the matter is a very new one, and it is hardly possible to say to-day how it will affect the problem of the method of evolution. If it be true, we must look upon sexual union as a conserving force rather than one for producing variability, and in general our conception of evolution will be much modified. At present, however, the subject, though perhaps as likely to be true as the hypothesis of Weismann, has not received the discussion or investigation which merits more than a notice at this place. But this notice serves at all events to show the uncertainty of Weismann's conception of evolution based upon the stability of germ plasm.

Returning to Weismann, there should be mentioned one curious phase of the theory as originally held by its author. If the germ plasm is absolutely stable, how could any variations ever have arisen? Certainly not by a mixture of germ plasms, for this would not produce variations, unless the two bits of germ plasm were unlike. In tracing variations thus to sexual union Weismann saw the need of some

earlier explanation to account for the difference between the hereditary material of different individuals. If the germ plasm is absolutely stable, how could it ever have acquired any differences? To answer this question Weismann found it necessary to trace all variations back to the far-distant past, before sexual reproduction began. In the unicellular animals, as we have noticed (page 164), since reproduction is simply division, all variations which might occur in the individual would be carried to the offspring. In these cases, therefore, acquired variations would be handed down from individual to individual, since there was then no germ plasm distinct from the body of the organism. By this means variations became introduced into the unicellular organisms and, when subsequently sexual reproduction began and the germ plasm became distinct from the body cells, this germ plasm was already provided with many variations in different individuals. According to Weismann's view, these variations were represented by material particles in the germ plasm, and all subsequent variations of all animals and plants have been produced simply by the different shuffling of these particles, no two mixtures ever producing exactly the same combinations. All variations of all times were thus traced back to the primitive world when only unicellular organisms existed. The animal and vegetable kingdoms have arisen from the continually changing combinations of the material particles in the germ plasm, each representing some variation, which appeared no one knows how many millions of years ago. Such a

position is certainly very extraordinary, and strikes us as almost an absurdity. Even Weismann in his later writings has abandoned this part of his theory, although still holding to the view that variation in general can be largely traced back to the unicellular organisms.

### *Stability—Evidence from Observations*

Purely theoretical discussion is usually fruitless, and in dealing with this subject from the standpoint of theory alone we can have little prospect of reaching any conclusion. Fortunately there are direct facts of observation which bear upon the matter, and which lead us to a positive result. Even Weismann, convinced by facts of observation, has yielded his original position, and now admits that this germ plasm is not absolutely stable. The reasons that have led him to this admission are indeed partly theoretical, such as have been considered, but chiefly the consideration of a series of facts which teach that the hereditary characters can certainly be modified, entirely *independent of sexual union.*

In accordance with the original theory it would of course follow that animals which develop without sexual union could have no congenital variations, and hence could have no evolution. But this is certainly not the fact. There are certain groups of animals and plants which may reproduce parthenogenetically, *i. e.*, the eggs develop without union with a male cell. This is, of course, reproduction without sexual union. But there is no reason to think that

the offspring fail to show variations. Better still for our purpose may be mentioned certain groups of low plants, including some of the seaweeds and probably the fungi, in which no true sexual union ever occurs. There are no sexual organs, and the reproduction seems to be universally without any sexual union. If sexual union does occur, it is certainly rare. Now, in accordance with the idea that congenital variation comes *only* from the union of germ plasm, there could be no variation among these plants, and consequently no evolution. But these plants show just as wide variations as do other plants, and they have certainly been subject to the same sort of evolution as have other plants. Here plainly enough congenital variations have occurred independent of the sexual process.

Still more significant, since the matter comes more easily under direct observation, are facts derived from what are called *bud variations*. A bud variation is one which occurs in a single bud upon a plant, and it may be only a slight variation from the character of the other buds, or it may be a very great one, such as would be called a "sport." Now in many plants buds are capable of growing into new plants. If a bud or a branch be separated from the plant and be put in proper conditions it will develop roots, and, in time, grow into a complete individual. When such a plant arises from a bud that has shown some variation from the original plant, the new individual, as would be expected, will show this variation. The variation will, moreover, now remain constant. The plant may be pro-

pagated by cuttings, or it may be allowed to produce seeds, and the plant thus be reproduced by sexual union. But in either case the new variety may appear in subsequent plants. In other words, these bud varieties are propagated just as truly as are variations from seedlings, and they become, therefore, congenital variations. Again and again horticulturists have produced new varieties by the selection of buds. The moss roses, for example, arose as bud variations, but are now just as truly distinct and just as truly propagated by seeds as are other varieties of roses which have arisen by sexual union. No one can distinguish between a bud variety and a seed variety. Such bud varieties, however, certainly have not come from sexual union, and, since they behave exactly like other varieties, we find here that congenital characters may arise from some other source than sexual union.

From these facts a few significant conclusions may be drawn. First, sexual union is *not* necessary to produce variations which shall be lasting and count in the process of evolution. Second, the germinal substance is *not* confined to the reproductive organs, since these bud variations evidently contain some of it. Third, the germinal substance which is in such a bud must be subject to variation independent of the rest of the germinal substance in the plant, since the offspring of the bud show the new characters, while the offspring of the rest of the plant show only the old characters. Clearly then the germ plasm has been modified by some forces acting upon it subsequent to the last period of sexual

union. It must be subject to modification by the direct action of the environment. The consideration of such facts has led Weismann and his school to admit that the germ plasm is subject to variation, either spontaneous and due to its inherent instability, or under the direct influence of its conditions, but in either case independent of sexual union.

To this extent then do we find essential agreement. The germ plasm is not absolutely stable. If we now free this statement from such hypothetical terms as germ plasm and ask what it actually means we find it essentially as follows: While the basis of heredity is something continuous from generation to generation, that something is not unalterable, but *the hereditary characters which an animal or plant may transmit to its descendants may be modified by conditions. They are not absolutely fixed by the original character of the hereditary material which the individual receives.*

But if we ask next how stable this substance is we meet widely different opinions. Weismann thinks it highly stable and only exceptionally modified by conditions. Bateson, in general opposed to Weismann, also believes it to be quite stable, and thinks that it swings from one point of stability to another. Williams, on the other hand, insists that instability is its essential character, and that it is always varying in one direction or another. Between such widely differing views no compromise can be made, and we need not dwell longer upon the subject.

## *Instability as Affecting Evolution*

It does concern our subject, however, to notice how greatly this admission of the instability of the germ plasm modifies our conception of the method of evolution. Instead of being obliged to depend entirely upon such congenital characters as come from mixtures of germinal traits in sexual union, we have an entirely new set of variations to aid in the process of evolution. Instead of finding that the environment counts for nothing in the process, except to determine which individuals shall survive, we find that it may count for a great deal in originating new characters, since it may produce variations in the germ plasm, giving us hence congenital as well as acquired variations. It is true that we have as yet seen no reason for believing that these variations would adapt the individual to new conditions. They are not, like acquired variations, the direct result of the organism reacting to meet its conditions. They would seem rather to be simply chance, indefinite variations in the unstable germ plasm, brought about by the fact that a change in environment disturbs the normal physiology of the organism. Such changes may or may not be adaptive. But even though not adaptive they do have this feature of importance,—they will be most likely to occur when most wanted. It is when the environment of the individual changes that there is the greatest need of a modification of the race. The fact that the individual must adapt itself to new conditions shows that a new adaptation is needed in

the race as well as in the individual. The changes needed in the individual are produced by acquired variations. To change the race the germ plasm must be modified. If, however, the germ plasm may be affected by the fact that the individual is somewhat out of harmony with its conditions, we see that the germ plasm will tend to begin to show variations when the individual begins to need new characters. In other words, if the germ plasm is really unstable and likely to be affected by changes in its conditions, then it will follow that congenital variations will be likely to appear when variation is needed, and this will be when acquired variations occur. They will appear when needed although they may have no special adaptability to the special need. The adaptability will come later by natural selection.

The importance of this change in the understanding of the facts of heredity is very great. The essentially new features of Weismann's theory of evolution were two. The first was the non-inheritance of acquired characters, and the second the idea that all congenital variations come from sexual union. With the admission on Weismann's part that the germ plasm is subject to other modifying influences besides sexual union, we are brought back to a position more closely resembling that held by Darwin. Darwin supposed that it is the constant changes in the environment which induce variations among organisms, congenital as well as acquired, and that these changes have been the foundation stones of evolution. To this position we return with

this change in the attitude of Weismann toward variations. Weismann's position is, however, still quite different from Darwin's, since he looks upon sexual union as the chief cause of congenital variations, and the direct variation of the germ plasm as secondary, and since he absolutely denies the possibility of the inheritance of acquired characters.

### *Perpetual Continuity of Germ Plasm—Theoretical Conclusions*

Having seen that Weismann has abandoned the absolute stability of germ plasm, we turn to the other problem of the transmission of acquired characters. Weismann has supposed that this germ plasm is continuous from generation to generation as something handed from parent to child, but neither added to nor subtracted from by the individual that carries it. There is thus no commerce between the germ plasm and the body. The body and the germ plasm have absolutely independent spheres of action, the body simply carrying the germ plasm, but having no further relation to it. It is upon this part of the theory that the claim of the non-inheritance of acquired characters is based. If the body does have commerce with the germ plasm, it would be easy to assume that acquired characters might impress themselves upon the germ material, but if there is no such commerce, then of course acquired characters cannot be inherited.

In the first place there is no logical reason why we might not suppose that such commerce takes place. When it is admitted, as we have just seen,

that the germ plasm may be modified by other conditions than sexual union, why may we not suppose that the variations in the body may directly affect the germ plasm? The germ plasm is stored in the body, and the conditions affecting it must be modified by changes in the body. The individual constitutes the environment of the germ plasm, and if this plasm is subject to change with its environment, it follows that changes in the individual, *i. e.*, acquired variations, may have some effect upon the germ plasm, and hence produce congenital variations.

This is rendered still more probable when we come to consider a new line of facts. As first conceived and as hitherto considered in our discussion, the germ plasm has been regarded as a material derived from the egg and stored in the reproductive organs until it again finds its way into a new egg of the next generation. But there is absolute demonstration that such is not a correct view of the facts. The germ material is not confined to the reproductive bodies. Among plants the facts that prove this are most striking. In most plants a branch is capable of reproducing the whole individual, a fact that shows that each branch must contain some germ plasm. This is perhaps not surprising when we remember that branches normally produce flowers, and might therefore be considered as containing the reproductive organs at all times. But there are many plants where smaller parts will produce the entire plant. Among most low plants it is a common rule for small bits of the plant to reproduce the

entire individual. A small bit of the moss from any part of the body will produce a complete plant capable of developing reproductive organs. This is especially striking here, since the moss has two distinct generations, and this small bit must therefore contain germ plasm representing both generations. Even among flowering plants the same thing is true. A small bit of a leaf of a begonia plant may take root and produce a complete plant capable of producing flowers, and therefore containing germ plasm. Now the leaf of the begonia certainly does not normally produce flowers, although this experiment shows that it certainly does contain the hereditary substance. Indeed botanists have found this property very widely distributed, and in nearly all plants small bits of the plant body—buds, twigs, branches, or leaves — may under proper conditions grow into entire individuals. Such individuals not only become like the originals in shape, but they develop sexual bodies with complete functions, and hence all must contain germ plasm. Here, then, we have demonstrative evidence that the germ substance is not stored in the reproductive organs alone. The leaf, the twig, the branch, or the root that is capable of producing the new plant must also contain it, and since this power of developing the new individual is found in all parts of the plant, it follows, of course, that the germ plasm, whatever it may be, is distributed among plants in all parts of the body. Instead of being confined to the reproductive organs, and through these handed down from generation to generation, it is found in all parts of the body.

Zoölogists do not find so much evidence for such a wide distribution of the germ plasm, at least among higher animals. Perhaps here is one reason why zoölogists and botanists are apt to disagree upon this matter of heredity. Among lower animals, however, facts similar to those described in plants are found. A small fragment of hydra can develop into a complete sexually mature individual, and it seems to make no difference from what part of the body the fragment is taken. The same is true of many worms and of some other low animals. Among higher animals we find this power of reproducing lost parts becomes less and less marked, and finally it almost disappears. In hydra a small bit can reproduce the whole animal. Among lizards the body can reproduce lost legs or lost tails by new growth, although they cannot reproduce the whole body. In such cases it is necessary to suppose that the cells of the body from which the new legs arise contain some of the germinal substance in a partially differentiated condition, but comprehensive enough to control the development of the new leg with its organs complete. It is perhaps not proper to say that the cells contain germ plasm, since they cannot produce the whole organism, but the difference between this case and that of hydra, where the few cells may develop the animal complete, is clearly one of degree and not of kind. Among higher animals still this power of reproducing lost parts seems practically to disappear. With mammals it seems that only bits of the reproductive bodies, *i. e.*, eggs, have the power of developing the whole animal

complete. Here there seems more reason for believing that Weismann's original conception is correct, and that the germ plasm is stored away in the reproductive glands.

In most lower animals, then, and in all plants, it is demonstrated that the germ plasm is widely distributed through the body. But this conclusion does not indicate that the germ plasm and the body are not independent of each other, each acting in a sphere of its own. The question whether the germ plasm is all collected in the ovary or whether it is distributed through all parts of the body, does not affect the idea of its distinctness in function and its continuity from generation to generation. Even though we do find it more or less scattered through the body, the idea of its continuity from generation to generation stands as firmly as ever; and, in spite of these modifications, the belief that the basis of heredity is to be found in the continuity of germ plasm has become more and more widely extended.

But while this is true it is evident that these new facts open a much wider possibility for modification of the germ plasm by external conditions. The ovary is commonly deposited in a thoroughly protected position in the body, where it receives little influence from the external world. If the germ plasm were simply stored within it there might be difficulty in believing that it would be influenced by environment. But since it is really distributed over the body, in all parts and perhaps in all cells, it is easy to understand how it may be modified by changes in the environment affecting the body.

This would easily explain the production of bud variations and their perpetuation by inheritance. Such buds must, of course, contain germ plasm, and this material, being at the end of the bud, must be exposed to the direct action of the environment. It would be here almost sure to be influenced by changes in the environment, and its variations would be transmitted to posterity.

Thus we find reason for doubting the absolute continuity of the germ plasm from egg to egg. It is certainly not continuous in the sense that it is handed down simply in the reproductive organs while the body develops in a sphere of its own. It is not continuous in the sense that an animal hands to its offspring exactly the same kind of germ plasm which it received from its parents. On the contrary, during the whole life of the individual this germ plasm is subject to new variations produced in it by the influences acting upon it directly. Such variations, of course, add to or take away from the characters of the germ plasm, so that, by the time the individual is ready to transmit some of it to his offspring in the reproductive act, the germ plasm is in some degree different from that which he received at his birth. Thus the conception of the strict continuity is in a measure disproved.

### *Inheritance of Acquired Characters*

After this somewhat speculative but necessary discussion we come finally to the direct question of the inheritance of acquired characters. Beyond doubt this is one of the most important questions

affecting the problem of evolution, since upon its answer hangs the question of whether the life of the individual has any influence upon the evolutionary process. The admission that the germ plasm is not absolutely continuous does not involve the inheritance of acquired characters. The difficulty of the matter lies just here: It is easy to believe that changes in the body may induce variations in the germ plasm, but it is extremely difficult to believe that they add to the germ plasm something which will induce in the next generation congenital characters similar to the acquired characters of this generation. How, for example, could the increase of size in the blacksmith's arm muscles affect that particular part of the germ plasm in his reproductive organs which is destined to control the growth of the arm muscles in the next generation, and affect it in such a way that the child should have larger muscles than the father had at birth? How could the reduction of an eye by disuse so affect the germ plasm that only that minute part of it which controls the development of the eye should be affected, and this in the way of reducing the eye in the next generation? We can conceive no answer to these questions.

But after all, the question must be one of evidence and not of ease of understanding. The whole phenomenon of heredity is absolutely a mystery, and we must not be surprised at the difficulty of understanding a particular part of it. We must then ask what is the teaching of the evidence upon this matter.

The first feeling of everyone is that a theory that denies the possibility of the inheritance of acquired characters cannot be true. This was the feeling of scientists when the problem was first forcibly brought to their attention by Weismann. Darwin had carefully studied the subject, and had arrived at the conclusion that we cannot deny the inheritance of acquired characters. We know from the treatment of the subject in his writings, and better still from reported conversations with him, that the whole question of the non-inheritance of such characters had been studied by him, and that he had reached the conclusion that occasional inheritance of acquired characters must be admitted. But to most scientists previous to Weismann's writings, the thought that acquired characters cannot by any possibility be inherited, and can therefore play absolutely no part in evolution, had hardly occurred, or had at least not been seriously considered. Acquired characters were the basis of Lamarckism, and many facts had been put upon record which seemed to be demonstrations of this inheritance. But in spite of such a general belief, the subject demanded an entirely new consideration in the light of the conclusions of Weismann.

It will be admitted by all who look into the matter that the seeming cases of inheritance of acquired characters have proved very illusive upon careful study. Just as soon as they are tested it proves that there is always a flaw in the evidence. Many instances which will occur to the mind of the reader will concern the inheritance of human mental ac-

quirements. All such cases must, however, be rejected, from the fact that the education and environment surrounding the offspring have such an extraordinary effect upon the individual as to make any conclusions as to inherited mental characters absolutely unreliable. Practically no evidence of value can be obtained from the mental attributes of man. The vast majority of instances of supposed inheritance of acquired characters among men disappear speedily when carefully studied.

When we come to ask ourselves what sort of evidence might be expected upon the supposition that acquired characters *are* inherited, we find it very difficult to answer. There is one kind of data which might settle the question if such data occurred. There can be no question that a mutilation which occurs from an accident is an acquired character. If such a mutilation were inherited it would be a plain case of the inheritance of an acquired character. But it is well known that mutilations are not inherited. A man who has lost a leg does not beget children with one leg, and it is so well known that such individual mutilations are not transmitted that it needs no further comment. But it might be thought that if the same mutilation should occur generation after generation it might, in time, affect the race. But here, too, we have plenty of evidence to the contrary. Circumcision has been practised among the Jews for thousands of years, and it has had no effect so far as the inheritance of the mutilation is concerned. In China the habit of dwarfing the feet of the girls has been followed for

hundreds of generations; but the Chinese girl of to-day is born with feet just as well formed as are those of the rest of the human race where this mutilation is not practised. Thus even long continued mutilations do not become matters of heredity.

There are, however, a few instances known which look like the transmission of mutilations, and two of these may serve us as illustrations of the illusiveness of the evidence. Weismann's attention was called to a girl who had inherited a scar on her ear. Her father had received a wound upon the ear while in the university, and his five-year-old daughter had a similar scar. It seemed like a plain case of the inheritance of an acquired character, until a careful study showed that the father possessed a somewhat similar mark on both ears, showing that he had also inherited them as congenital characters. He had evidently transmitted to his daughter a congenital character which he had himself inherited, the accident of the wound simply serving to call attention to it. Another case which has been frequently cited is that of a cow who lost a horn from suppuration, and subsequently produced offspring showing an apparent inheritance of this mutilation. But Weismann pointed out that the loss of a horn in this way is a very unusual thing, and indicated in all probability, that the cow had some congenital peculiarity which rendered her horns especially liable to disease. In other words, she probably lost her horn not because of the disease attacking it, but in reality the disease attacked it because she had inherited here some congenital weakness. This congenital

weakness she would, of course, transmit to her offspring, and thus the calf would inherit, not the mutilation which the mother suffered, but rather the congenital weakness which the mother inherited. Now while there is no proof that this explanation of Weismann's is correct, since the instance occurred before there was any chance to study it in the light of modern ideas, still it is so evident that the explanation is a plausible one, that it is generally admitted that it is satisfactory, and that those who wish to believe in the inheritance of acquired characters cannot base any argument on this particular case. Practically the same may be said of all other instances of mutilation. There is no satisfactory evidence that they are inherited, and this position is admitted by all.

After we have ruled mutilations out of account, the problem of getting evidence of acquired characters being inherited becomes very difficult, and indeed well-nigh impossible of solution. The difficulty comes in telling what is an acquired character. The effects of use and disuse are certainly examples of such characters, and there are plenty of instances which seem most easily explained by the inheritance of such characters, as, for example, the increase of the middle toe of the horse's foot or the loss of eyes in cave animals. But if an organ be used it is evidently of value, and the moment we admit it to be of value that moment we make it possible for the Weismannian to say that it has been developed by the principle of natural selection, since all useful organs come within the reach of this force. We

have already noticed how natural selection is applied to the development of such characters as the adaptation of the monkey's hands for climbing, etc. Since, then, the development of an organ that is used is open to both explanations, it cannot be regarded as proof of the inheritance of the effects of use, especially when we remember that useful organs develop in the same way among plants where the principle of increase by use cannot apply. The reverse side of the problem offers no better hope, viz., the loss of an organ by disuse, for the principle of panmixia is brought forward at once to account for the degradation of organs which are not of selective value, and here, too, we must remember that the same phenomenon occurs among plants where no principle of disuse can come into play.

It might be supposed that we could find some test cases in connection with the direct effect of the environment, such as climate or food. If all the trees in America have a general tendency to show variations in definite lines, in spite of their not very close relationships, what could be more clear than that the climate or soil of America produces a definite variation in certain directions in all cases? It is true that nothing can be more clear than this conclusion, but the further conclusion, that such effects are matters of inheritance, is not so clear. If such trees are put into a different climate they rapidly change their character, and it is, therefore, by no means sure that these characters are inherited race characters. They may be simply acquired characters, acquired independently by each individ-

ual as the result of the conditions acting upon it and independent of inheritance. If seeds of such plants were taken to a very different climate and it were found that these climatic characters were retained in the new territory, then we might claim that they were fixed in the race by inheritance. But such evidence is not at hand. When seeds are transported to different countries and develop under new conditions they depart rapidly from the American types, and assume new variations. It is as yet impossible to say what characters are inherited and what acquired, and thus this instance fails to be convincing.

The difficulty of determining what is an acquired character is almost insurmountable. It is made more difficult by the fact that the Weismannian school now admits that the germ plasm may vary independently of sexual union. Hence, if an absolutely *new* character should develop in any individual, there is no way of proving it to be an acquired character. It is always possible to suppose that it has arisen as a congenital character, due to some variation in the germ plasm, even though it be something absolutely new in the race and apparently due to environment, and hence acquired.

Thus it is that the discussion over the inheritance of acquired characters has hitherto failed to reach any positive conclusion. The disputants on each side insist that the burden of proof lies with their opponents, a procedure which does not advance matters at all. The opponents of Weismann bring forward many instances which they think indicate an

inheritance of acquired characters. They instance the almost universal belief of mankind, the uniform belief of breeders, and the even more constant belief of horticulturists. They point to the many instances where development occurs along lines of use and disuse; they show how species are modified by climate; they show how animals and plants in new climates acquire independently new characters. But all this fails to reach the centre of the question. They are told that a general belief does not count at all in the matter; that some of these inherited characters are not acquired. They are told that many of the characters under discussion are not inherited at all, but simply developed independently by each individual. They are told that such characters as are really inherited can just as well be supposed to have been originally brought about by sexual union and preserved by natural selection.

The discussion has gone on merrily for fifteen years without reaching a conclusion much more satisfactory than at the outset. Neither side has proved its case, and each is to-day confident of the justice of its position. Certainly the inheritance of acquired characters has not been proved, and on the other hand its possibility has not been disproved. It must not be inferred from this statement, however, that this fifteen years has not changed the attitude of scientists toward the problem, for both Weismann and his opponents hold different positions to-day from those held at the beginning of the discussion. Those who believe in the inheritance of acquired characters will freely admit to-day that

such inheritance is not common, that it does not concern mutilations or incidental effects, and it is only when the effect is considerable and long continued that there is any probability of its being transmitted by inheritance. They admit, in short, that the agency of acquired characters has not played the important part in descent which they were at one time inclined to believe. On the other hand, the adherents of Weismann will in their turn make the admissions, which we have noticed, of the independent variability of the germ plasm and its possibility of modification by the environment which makes external conditions and, indeed, ac quired variations, to a certain extent direct facto in evolution. But while each admits that its view have been somewhat changed, they are as far apa as ever upon this fundamental matter of the heritance of acquired characters, the one side de ing the possibility of such inheritance and the ot claiming that it is occasionally a fact, and her force in evolution.

There is some reason for thinking that a p this wide difference of opinion is due to the fa different students have studied different cl organisms. The botanists appear more th convinced of the possibility of the inhe acquired characters than do the zoölo tainly many leading botanists feel it admit the possibility of such inheri culturists insist that they can a variations among plants by chang tions of cultivation, *i. e.*, acquire

then can select the individuals showing these variations and find them breeding true by seed, *i. e.*, showing congenital variations. They succeed in dwarfing plants by poor nutrition, and find that the stunted characteristics remain true in following generations for a time, in spite of the fact that the later generations are well nourished, thus showing that the influence is transmitted by heredity. It is claimed by them that many of our cultivated varieties, which now breed true, were originally produced by the selection of acquired varieties, and are thus examples of the inheritance of characters pro- luced originally by extrinsic rather than intrinsic orces. The zoölogists, on the other hand, find less vidence for such inheritance. Without insisting pon the point, this may perhaps be due to the fact at the two kingdoms are differently constituted in s matter of germ plasm, a conclusion quite in ac- dance with the fact already noticed of the wide ribution of germ plasm through the tissues of plant.

### *Weismann's Theory as it Stands To-Day*

vident that both Weismann's theories and he Lamarckians are considerably modi- heir earlier position, and it is desirable ire into the present position of each. heory of heredity has been very greatly admission of the independent vari- rm plasm and its dependence upon this makes it no longer necessary

to regard sexual union as the sole source of the evolutionary process. But even with this change the fundamental feature of the theory is retained. It is still recognized that the germ plasm is the sole basis of heredity. It is still believed that this germ plasm is carried from parent to child, chiefly in the reproductive organs, at least in animals, and is stored in the individual for the next generation with comparatively few changes. It still appears that the next generation will be like the last, because it has developed as the result of the unfolding of the powers of a bit of the same germ plasm It still follows that the individual inherits most of its characters, not directly from its parents, but from this continuous germ plasm that is carried from age to age. Continuity of germ plasm still remains as the basis of heredity. The fact that we have been forced to believe that the germinal substance is not absolutely stable does not interfere with its being properly regarded as continuous and as the basis of heredity while the possibility of some commerce between the germ plasm and the body rather removes than makes difficulties. In short, the valuable parts of Weismann's theory remain while some of its troublesome and unnecessary features have been removed. The value of the theory is in its presenting such a simple method of comprehending the hereditary process, and the reason for its wide acceptance is its simplicity, together with its confirmation from microscopic study. With the admission of some instability in the germ plasm and of a possibility of commerce between it

and the body, it is questionable whether the theory is really new, since an almost identical view was earlier advanced by Galton and called the theory of "stirp." But with the question of priority we need not concern ourselves. The conception of the process of heredity that is left to-day is a continuity of a tolerably constant but somewhat variable germ plasm, which is handed down from generation to generation, and which is capable of modifications produced in it either by sexual union or by the direct action of the environment. Evolution of organisms has been brought about by the selection of the favorable variations in this germ plasm.

This is essentially the position held to-day by the conservative naturalists. Of course there will be found a variety of opinions in many details, but practically all scientists acknowledge that Weismann and Galton and Brooks reached a fundamental truth when they pointed out that the basis of heredity is a continuous germinal substance, and all recognize that this conception has wonderfully cleared our ideas of nature's methods of reproduction. All would admit that this substance is carried from generation to generation. Most would regard it as relatively stable in its nature, but open to a variety of influences which may change its nature and, therefore, induce congenital variations. The first of these is sexual union; but in addition there are a variety of influences that affect the germ plasm, independent of sexual union; and some look upon these secondary influences as of more importance than sexual union. That acquired characters

can be inherited is regarded as doubtful, at least in the case of the higher animals.

### *Lamarckism as it Stands To-Day*

What of the present attitude of science toward the Lamarckian factors which have been so decidedly discarded by Weismann? So long as the possibility of the inheritance of acquired characters is left unsettled there can be no unanimity of agreement in regard to the agency of these factors. Those who are inclined to believe that acquired characters may, under certain conditions, be inherited find in the Lamarckian factors important aids in evolution, while these factors are of course denied absolutely by those who think that acquired characters cannot be inherited. There is no compromise between these two positions, which are mutually exclusive. No decision between them can be reached until the fundamental question of inheritance can be settled.

Meantime it is evident that less insistence is being placed upon the Lamarckian factors than was the case a few years ago. The adherents of the Neo-Lamarckian school, of course, still insist upon the importance of these characters. But their uncertainty, the lack of good evidence that acquired characters can be inherited, the absence of proof that use and disuse affect posterity, have together led naturalists, even those who accept the Lamarckian factors, to regard their importance as less than believed a few years ago.

This lack of confidence is increased by the conviction that even if the inheritance of acquired characters is admitted, this will only partly solve the difficulties which evolutionists meet. There is in the first place the problem of explaining why an adaptive character should arise even as an acquired character. Why should the skin become dark when exposed to the sun? Why should organs increase in efficiency with use? Why should muscles grow when exercised? These are pertinent questions to the biologist who thinks he finds in the Lamarckian factors the explanation of evolution. They may, however, be passed here since they are manifestly part of the subject of the organic constitution of living matter, which is certainly not yet understood. But, further, the influence of use as increasing the size of organs, even if admitted, gives little aid in solving many difficult problems. Plants do not use organs, nor can we believe that they lose them through disuse; but here, just as among animals, the reduction of useless organs is a rule. If use inheritance can count for nothing among plants, it is certainly doubtful whether it is a real factor among animals. Further, use inheritance fails to aid in explaining the beginnings of organs. An organ cannot be used until it has appeared. Training does not produce *new* muscles, though it may increase the efficiency of those in existence. Thus here the same difficulties arise for the Lamarckian as for the Weismannian. In other words, even granting the Lamarckian factors of use inheritance, there is evidently something more needed to explain

the origin of species which is found neither in Lamarckism nor in natural selection.

As concerns the other Lamarckian factors, the matter stands somewhat differently. These factors are chiefly the direct effect of climate and food upon the individual, and through him upon the race. Although these are called Lamarckian factors, since they imply the direct action of external agencies in producing variations and thus affecting evolution, they were hardly recognized in Lamarck's original theory, which placed so much stress upon use and disuse. In regard to the influence of food and climate, there is not a little evidence that such an influence may affect the race. A change in food has certainly been known to produce changes in the individual, which are followed by similar changes in following generations. Moreover, as we have seen, there is no logical difficulty in believing that climate and food may directly affect the germ plasm in such a way as to produce in it variations which would, of course, appear in following generations by inheritance. Weismann himself acknowledges that climatic changes may modify the germ plasm in such a way as to give rise to congenital variations at once which are similar to the characters produced in the individual as acquired variations. Allen has shown that the length of the bills of birds varies with the climate, a fact so universal that it must be due to the direct effect of climate. Now if such external conditions do affect the germ plasm, and should continue for many generations, it is evident that they might continue to produce greater

and greater influence upon the germ plasm, and this would mean that generation after generation would have a tendency to show variations along similar lines. This would give rise to determinate variation. Such an effect would not be due, however, to the action of the environment in producing an acquired variation in the individual, which was subsequently inherited, but rather to the direct effect of the environment upon the germ plasm, producing variations in it which induced congenital variations in all following generations. While, then, naturalists are laying less stress upon use inheritance as a factor in evolution, they are not so ready to give up this other direct action of the environment to produce congenital variations. But, admitting thus the environment as a large factor in causing variations which are inherited, we come back almost exactly to the position of Darwin, who looked upon variation as universal, and as due doubtless to many conditions which we do not know, but primarily dependent upon the changing action of the environment.

### *Mental Phenomena*

There are no phases of the evolution problem more closely connected with Weismann's theory of heredity than those relating to mental problems. The solution of evolution is, of course, not complete without its explanation of mental as well as physical phenomena. Mental characteristics, especially instincts, are just as truly specific charac-

ters as are bones and muscles, and must as truly be comprised in the method of evolution. But the problems connected with this subject have been especially perplexing.

We notice in the first place that among animals there have been two quite different lines of development of the mental nature, the one called instinct and the other intelligence. Instinct and reason are quite distinct from each other although inextricably associated in higher animals. With all instincts we find a little grain of intelligence, and with all animals guided by intelligence, even including man, there may be detected not a little instinct. But in their nature instinct and reason are so different from each other that neither can be regarded as derived from the other. The high development of instinct is incompatible with the high development of intelligence, and *vice versa*.

Each of these phases of nervous phenomena has been adopted by different groups of animals. While it is the higher vertebrates, and especially man, that have developed intelligence, instincts have culminated in insects. The essential character of instincts is that they are inborn and not acquired by the individual. They must therefore be represented by some structure in the nervous system. They are only slightly subject to improvement by intelligence, and are essentially alike in all individuals. They are for the evolutionist, therefore, just like the eye, characters whose method of origin must be explained in any theory of evolution. The origin of intelligence is also a matter of very difficult

solution, perhaps even more difficult than the origin of instincts. It is a subject entirely too broad to be considered in this work.

### *Instincts*

There are some phases of the problem of the origin of instincts so closely related to the topics which we have just been considering that they must be mentioned here. In the study of the origin of instincts we must consider them just as we would any other complicated structure, and expect to find a somewhat similar explanation. But there appears to be a very serious difficulty here in the fact that instincts are in many cases very complicated, involving the harmonious action of a large number of parts together. It is thus impossible to believe that they have arisen by any single sudden variation. To assume that such a complicated instinct as that of nest building has arisen by a single variation, of course, begs the whole question, since it at once assumes that there are some unknown forces in the organism capable of producing complicated and adapted structures, which is the very thing that evolution is trying to explain. In the explanation of the origin of the eye, as we have seen, we account for the adaptation of the completed organ by the supposition of a gradual growth from a simpler condition, and the slow modification of the simple organ into a more complex one, every stage, however, being a complete organ and with functional activity. Now these complicated instincts have equal com-

plexity and equal adaptation. Witness, for example, the harmonious action of the instincts which control a beehive, or the instinct which impels certain wasps to sting other insects in order to paralyze them or kill them as food for their young, even though the wasp never sees her young. But, on the other hand, in regard to many of these instincts, it is impossible to conceive how they could have been developed by numerous intermediate steps. Here, then, is the difficulty. To assume that the germ plasm has suddenly become so modified that the next generation would develop such complicated instincts as the stinging of insects to prepare them as food for the unborn young, is to force us practically to assume that the germ plasm is intelligent, and this is of course an absurdity. This is, in short, to abandon all attempts at an explanation. There is nothing left but to conceive that they have been built up by slight steps, each of which has been of value enough to be preserved by natural selection. This is, of course, the position which naturalists adopt and which they are trying to substantiate to-day by renewed studies of instincts.

That the problem does not appear to naturalists to be insurmountable is evident from the fact that the special students of instincts think their origin capable of explanation. In the first place, it is to be noticed that the highly developed instincts are found chiefly among insects. Instincts are of course found among other animals, but nowhere so highly developed as among insects, and, moreover,

most of the perplexing cases of instincts are among animals of this class. Now it is at least suggestive to find that insects are the most abundant of animals. Five sixths of the species of animals are said to be insects. Moreover, their rate of reproduction is prodigious. No high development of instincts is of course possible except in animals with a well-developed nervous system, and no animals with a highly developed nervous system have a reproductive capacity equal to that of insects. This high rate of reproduction exposes these animals to an excessively severe struggle for existence. Since a fly may produce many thousands of descendants in a few weeks, it is evident that the vast majority must die without reaching maturity.

It is not without significance to find instincts developed most highly among animals which reproduce most rapidly, while intelligence is developed among those that breed more slowly. With a high rate of multiplication the principle of natural selection of course acts very rigidly. In other words, there is no group, among the higher animals, where the law of natural selection acts with such constancy as among insects, where the instincts are so highly developed. So far as this indicates anything, it seems to point to natural selection as the primal factor in the development of instincts. If intelligence had been an important factor in the origin of instincts, we should expect to find them more developed among the more intelligent animals. But finding them best developed where natural selection is most rigid gives *a priori* grounds for looking upon

natural selection as a prominent factor in explaining them.

In explaining the origin of instincts three great principles have been recognized. They are *natural selection*, *lapsing intelligence*, and *organic selection.* The first two were suggested by Darwin and the last by recent students of evolution. Noticing first the principle of natural selection, we find that its action in the origin of instincts is so similar to its action elsewhere that no extended notice is necessary. It is supposed that, with all the variations which are constantly occurring in animals, there are some in the structure of the nervous system as well as elsewhere. These variations in the nervous system lead to different habits on the part of the individuals, or, in other words, to inborn habits, or instincts. If such a new habit should be useful it would be preserved by natural selection. If it were due to a variation in the germ plasm it would of course be transmitted to following generations. Natural selection would thus preserve congenital variations of habit which would be instincts. If now we can imagine the complicated instincts to be built up by the accumulation of numerous small steps, each of use to its possessor, it is clear that natural selection would account for the origin of instincts just as well as it can account for the origin of the eye. It is only necessary to show that an instinct may have been developed by small steps, each of which is useful, in order to bring it under the law of natural selection.

But this appears, according to our present know-

ledge, extremely difficult to do. Most instincts are useless unless many parts act together in harmony, and it is very difficult to conceive them to have developed by small steps. The chances are very great against there occurring, at the same time, fortuitous variations giving animals an *instinct* to live in trees, and others modifying their organs in such a way as to *adapt* them to living in trees. It would seem as if there must be some agency which could associate together habit and structure in a way that simple chance could not do. For this reason Darwin, and after him Romanes, called to their aid the principle of *lapsing intelligence.* This suggestion is based upon the two facts that, (1) instincts are not invariable and, that (2) along with the instincts may always be found a little grain of intelligence. Animals that have definite instincts are found to modify them slightly to adapt them to new conditions. Birds change the character of their nests according to the locality where they build them. This can only be done by perceiving the relation of means to end, or, in other words, by intelligence. Now, if reason can thus modify the instinct of an animal, may it not be that we have in this factor the needed agency to guide the development of instincts? An animal may inherit an instinct leading to a certain line of action; but his intelligence leads him to modify this action in a slight degree in such a manner that, during his life, his habits show a slight improvement over this purely inborn tendency. This improved application of the inherited instinct will be repeated by the next generation also as an intellectual act.

Thus, for generation after generation, we may suppose the slight reasoning powers that an animal possesses enable it to modify its inherited habits. In time the modification in turn becomes a part of inheritance, and thus the original instinct has added to it this new modification which arose first as an act of slight intelligence. When this occurs the reasoning faculty no longer plays a part at this point, and the new modification of the habit of life becomes part of the instinct. The intellectual factor has "lapsed." If we may thus imagine the slight reasoning powers which the animals have to be used in changing little by little the original instincts, improving them slightly here and there to meet new conditions, it is possible to conceive that some of the complicated instincts have been built by slow steps. Intelligence would thus aid in adapting instinct to structure, and use would adapt structure to instinct. We should have little difficulty in understanding the slow development of complicated habits which become more and more complex as the intellectual factor adds a little with the successive generations. This does not mean, of course, that at any time such actions have been intellectual actions as a whole. It does not mean that insects formerly performed by intelligence the complicated actions which they now perform by instinct. It simply means that their intelligence, slight as it is, has been sufficient to enable each generation to change slightly the habit of the animal, so that the inherited instinct may be sufficiently modified to adapt it to new conditions. Intelligence has added a little with the

successive generations, but has never comprehended the whole at any time.

Now two things appear at a glance: First, it is clear that this principle of lapsing intelligence would be of great aid in explaining instincts if it could be accepted as a real factor. It would show how instinct and structure could develop together and how harmonious actions could be combined. But it is secondly evident that it would involve the inheritance of acquired characters. A change in habit produced by intelligence is an acquired character, while instincts are inherited, and only upon the principle that acquired characters can be inherited could such a modification of an instinct become itself part of the instinct.

There are certainly among animals some instincts which have been supposed to have originated in this manner. For example, the herding instinct of shepherd dogs. An animal of this breed does not drive sheep in the ordinary fashion, but contrives to keep them moving together in a mass. Now this habit is certainly an instinct, since it is found that young dogs, who have never been taught, have the same method of driving sheep the first time they see them. It has been natural to suppose that the habit was originally taught the dogs by the shepherd. It is certain that the shepherd does train the dogs to care for his sheep in the most skilful manner, and it has been natural to assume that such training was the origin of this instinct. If this is a fact, it is a case of lapsing intelligence. Many other instances might be given where intelligence seems to have been a factor.

But the uncertainty as to the inheritance of acquired characters places lapsing intelligence in doubt. There can, of course, be no doubt as to the position that the Weismannian school must take. Denying the possibility of the inheritance of acquired characters, they must deny the truth of lapsing intelligence. The instances of its supposed action must be explained by selection. In the case of the shepherd dog, for example, it is not difficult to find such explanation. Chance congenital habits are constantly arising among dogs, and the shepherd preserves and breeds from such dogs as show congenital habits best adapted to his needs. Selection has thus eliminated from the race all dogs that did not develop the proper instincts. This is of course a negative factor explaining the survival, but not the origin of instincts. Their origin must then be explained by the claim that the shepherd had for great numbers of generations been selecting such dogs as chanced to show instincts best suited to his fancy, and thus built up the instinct by an accumulation of numerous slight stages. We have no historical evidence to tell us whether this has been the case or not.

But if we give up this principle of lapsing intelligence we are in great perplexity at once. It is difficult enough to believe that some of these complicated instincts could have developed by successive stages even when guided by intelligence; it is practically impossible to believe that natural selection could have developed them alone by simply exterminating such animals as did not chance to present favorable congenital habits. The difficulty is especially great

because of the complexity of instincts and because of the necessity of their combining the harmonious action of many parts. For example: there is an inherited character of the frog which leads him to balance himself completely even after the cerebrum (*i. e.*, the intellectual part of the brain) is removed. Such a frog, with no volition, will balance himself upon a book, and if the book be slowly turned he will change his position, always crawling upon the top and keeping himself in an upright position. There is every reason for believing this to be an inherited power. But how could this habit have been developed? Frogs learn to balance themselves during life, and, if we could assume that such habits could be inherited, the explanation would be simple. But how could the selection of accidental congenital habits have produced the result? The action is a very complicated one, involving the use of many muscles working in delicate association with the sense organs. Such a harmonious adjustment of sense and muscle can hardly be supposed to have resulted from fortuitous variation, nor, on the other hand, can we conceive how it could have been developed by slight stages. Unless the parts all act in harmony there can be no result. To have been preserved by selection it is necessary that this complex series of muscle actions should, at the very outset, have been so well co-ordinated as to produce results of selective value. It is hardly credible that there could have been an accidental variation of the germ plasm offering, at a single generation, such a wonderfully complicated and har-

monious series of muscle actions. It is simply impossible to believe that such a combination could have appeared in many individuals at once, which, as we have seen, is necessary to explain its preservation by natural selection. It is equally impossible to conceive how such an action could have arisen by the preservation of intermediate steps, each of which was of selective value, for the action is without significance until it is co-ordinated. Natural selection without the aid of intelligence appears absolutely inadequate to meet the case. Those who have given most attention to the study of instincts appreciate this difficulty most seriously, and it is frankly admitted that to put the burden of explaining instincts upon natural selection alone, unaided by intelligence, is to lay upon it a load too heavy for it to carry. This is admitted even by those who feel that they cannot use the inheritance of acquired characters to help them out of the difficulty.

This dilemma has brought forward a third factor in explaining instincts which still uses intelligence as a force, but without the necessity of admitting the inheritance of acquired characters. This is the theory of "organic selection." This subject is considered in some detail in the next chapter, and will for the present be postponed.

## *Summary*

The theory of Weismann sharply separates the so-called Lamarckian factors from the Darwinian factors. The Lamarckian factors are those forces

which produce modifications in the individual directly and are then transmitted by heredity, while the Darwinian factors are those of selection, chiefly natural selection, which preserve variations that appear in the germinal substance and thus affect the individual only through inborn traits. To the Lamarckians the primary factors in evolution are external phenomena, such as heat, light, cold, climate, use, parasitism, etc., which directly affect the race, selection being secondary. To the Weismannian the primary factor is selection in its various forms, acting upon variations produced by internal causes. The one method of evolution is based upon modification by conditions, the other upon reproduction. The Weismannian school is, by its own theory, prevented from receiving aid from the Lamarckian factors and forced to explain evolution wholly by the selection of variations in the germ plasm. This school, therefore, finds itself confronted by all the objections which have been so earnestly hurled against natural selection as a sufficient cause of evolution. The chief of these obstacles lie along the lines of the doubtful utility of many specific characters, the evident tendency toward elimination by cross-breeding, the difficulty of explaining the beginnings of organs and the apparent existence of determinate variation. None of these obstacles is satisfactorily overcome by the school that bases the whole process of evolution upon natural selection of variations of the germ plasm which arise from sexual union. Scientists, Weismann included, have felt forced to find, either some new factor in hered-

ity, or some new factor in evolution. Weismann has stated that " the Lamarckians were right when they maintained that the factor (*i. e.*, natural selection) was insufficient for the explanation of the phenomena."

In asking which of the two horns of the dilemma to seize, we have first asked whether Weismann's theory of heredity, denying, as it does, the inheritance of acquired characters, is substantiated. It has appeared that the theory is both a theory of heredity and a theory of evolution. As a theory of heredity it is based upon the continuity of germ plasm, and as such it is so simple and so in accordance with facts that it has been accepted with practical unanimity. As a theory of evolution it is based upon the further conception that (1), this germ substance is absolutely stable and capable of modification only through sexual union; and (2), that there is no possibility of commerce between the germ substance and the body of the individual carrying it as a legacy to the future. These two conceptions forced Weismann to found the whole process of evolution upon the selection of congenital variations produced by sexual union. But the study of nature soon forced him to abandon the first conception and to admit that this germ plasm is subject to a certain amount of variation as the result of the action of the environment upon it. This opened the way to the possibility of the environment having a direct, as well as an indirect, influence upon the process of evolution. The question whether there could be any commerce between the body and the

germ has not been so easy to answer. That the germ plasm may be indefinitely modified by unusual conditions of the body seems quite likely, but it is hardly conceivable that an acquired variation of any organ can have such an effect upon the germ plasm, stored in the reproductive organs, that just that part of the germ plasm shall be modified that controls the development of the organ in question, and shall be modified in such a way as to repeat the acquired variation in the next generation. Satisfactory evidence for the inheritance of acquired characters has not, up to the present time, been found, although botanists are quite confident that it occurs in plants.

Meantime it has become manifest that these Lamarckian factors, even if admitted, are not of so much value as has been conceived. Use and disuse do not apply to plants, where we find the phenomena to be explained of equal difficulty with those of animals. Further, it has appeared that many of the puzzling problems of evolution, such as the development of useless characters, the beginnings of organs, etc., are no more easily explained by the Lamarckian than by the Darwinian factors. While the Lamarckian factors might aid materially in some problems, in many others they are even more inadequate than the Darwinian factors. The most serious puzzles of evolution are not satisfactorily met by either Lamarckism or Weismannism. Especially is this true in the problem of the origin of instincts, for here admittedly natural selection is inadequate and the inheritance of acquired charac-

ters not proved. Seemingly, then, while we may perhaps some day find that there are other factors in heredity, we must seize the other horn of the dilemma, and see if we cannot find some other factors in evolution. To this question, therefore, we next turn our attention.

# CHAPTER VII

## RECENT ADDITIONS TO THE THEORY OF EVOLUTION

IT has become more and more clear that the problem of the method of the evolution of species is not yet solved. Natural selection of congenital variations is a prominent factor, but the difficulties which we have noticed have forced most naturalists to the conclusion that it alone cannot be regarded as sufficient to explain the origin of species, and it must, probably, be admitted that this number is increasing among the younger naturalists, at least in America and Germany. The Lamarckian factors are uncertain, and, even if accepted, fail to meet all classes of problems, and are of less value than at one time considered. The fact that these two older theories leave many problems unsolved has become more appreciated, and to-day naturalists are actively searching for something to aid in the solution of the problems. We find it freely admitted that we need something more before we can feel that we understand even the fundamental aspects of the method of the origin of species, and we are beginning to find

references to the "unknown factor" in evolution. Of course to some classes of thinkers this "unknown factor" will at once be said to be *design*, and the admission of biologists that they are not satisfied with the present explanation of evolution will be hailed as an argument for design. The naturalist will, of course, insist that the unknown factor will be found among natural forces. In all directions do we find this exploration continuing. Some naturalists are ostensibly hunting for new factors of evolution; others are quietly searching in new directions in hope of finding some aid in explaining the general problem of life. Some of them relegate natural selection to the past as "the refuted Darwinian theory." Some announce it as their opinion that natural selection is incapable of giving any further light upon the origin of species; while others are only trying to find new conditions under which natural selection can act in such a way as to be more efficient. But on all sides there is a feeling that we need something more than Darwin discovered. With the exception of a few extremists no one appears thoroughly satisfied with our present information as to the methods of evolution or with the present known laws and forces regulating the origin of species. It is significant to find that it is among the younger men where this dissatisfaction is most expressed, and among them where we find the strongest conviction that something more remains to be discovered. Some of them believe this unknown factor or factors will soon be found. One of the foremost of young experimenters, however,

says that it is not only unknown but unknowable. It remains for us to see in what directions the new search is being conducted.

Foremost among the recent additions to the theory of evolution stand two important suggestions. They are the Theory of Isolation and the Theory of Organic Selection.

### *The Theory of Isolation*

*Value of Isolation.*—Beyond doubt, one of the most important contributions to our understanding of the method of the origin of species that has been made since Darwin is in a series of suggestions, coming from several students independently, but all centring around the general idea of isolation. Unlike some of the recent additions to Darwinism, this principle of isolation is one the importance of which is acknowledged by everyone, no matter what his views may be in regard to other factors. It is of such importance that it deserves to rank with natural selection and Lamarckism as a third great theory of the origin of species. Different scientists differ as to the extent of the application of this principle of isolation, but all acknowledge its weight. The essence of the theory is that in the formation of species some individuals have been separated from the rest of the species and have subsequently developed by themselves.

Before considering the theory itself it will be best to notice the arguments which have led to the belief in the necessity of isolation. The first of these is

the recognized swamping effects of cross-breeding already referred to. This difficulty for natural selection, as we have seen, has been so great as to compel the abandonment of the idea that single variations can count for anything in the process of evolution. It is an absolute certainty that single variations cannot perpetuate themselves if there is free possibility of breeding with unmodified members of the race, for cross-breeding will soon eliminate them. Hence it has been necessary to assume that evolution has advanced by variations around a mean, that natural selection has simply preserved variations above or below the mean, and thus works upon large numbers of individuals rather than upon isolated variations. But now we must notice that the result of such an evolution, by selection of individuals above or below the mean, will be to advance the whole race along some definite line and could not produce a *divergence* of character among the descendants. The gradual raising of the mean character would give a continually advancing line of descent, but could never produce two divergent lines. It would produce what has been called *monotypic* but not *polytypic* descent. If there is anything certain in the descent theory it is that there has been a divergence of descent. Everything shows that species have arisen from common ancestors from which they diverged by descent. Now if it is true that natural selection can only act upon averages, and thus can simply elevate or lower the mean of any character, it is evident that this cannot produce divergence, and it is further evident

that some addition must be made to that theory before it is capable of meeting the actual conditions of descent. There must be some way of showing how the descendants from a common ancestor may have not only advanced in character, but also diverged into two or more different lines of descent.

Now it is evident that, if we could imagine an isolation of small groups of individuals from others, we should have conditions which would make divergence possible. If children of the same parents were forced to breed with each other, any peculiar characters which their parents had would tend to be retained rather than eliminated by cross-breeding. We have abundant evidence that such is strictly in accordance with the facts. A breeder of animals or plants, when he wishes to preserve a variation which may appear, takes care that individuals with similar variations shall breed together, with a result that is seen in the great variety and extraordinary characters of our breeds of domestic animals and plants. Domestic varieties are always produced by isolation. Moreover, we have equally good evidence that such isolation in nature produces similar results. Most excellent illustrations of the principle are offered by oceanic islands which are so far from the mainland that visits by immigrants are very rare. The offspring of the few individuals which do reach the islands are forced to breed together. The isolation thus produced gives an opportunity for the peculiarities of the individual to develop, unchecked by the obliterating effect of cross-breeding with the average individual, and the result is the development

on such islands of many odd types which may present very unique characters. On the Galapagos Islands for example, the turtles have grown to weigh several hundreds of pounds, and sometimes have their toes covered with hoofs. Such peculiarities could never have been developed where free inter-breeding of individuals could occur, first because cross-breeding would eliminate them, and second because natural selection would cause their disappearance. Only under conditions of isolation therefore could such variations become developed.

Recognizing, then, the great influence of isolation in producing the development of new types it is clear that we may find here the secret of the divergent evolution which characterizes nature. Natural selection, acting upon a large number of individuals in a given locality and living under similar conditions, will not produce several new species among the descendants, but will simply advance the whole group of organisms along the line of greater adaptation to their conditions. Divergence must be due to a prevention of inter-breeding. If we can understand some method of explaining how the individuals might be separated from each other, so that those with a certain general character would be unable to cross with others not possessing the character, we can understand how two different lines of descent would arise and two different species would result. With such isolation of groups of descendants from a common parent, it is easy to understand divergent evolution and the origin of species from common centres. Without it, it is very difficult, or, indeed,

impossible, to understand how there can be anything more than evolution along a single line, the advance of all individuals together toward higher grades of adaptation but without divergence.

### *Methods of Isolation*

*Geographical.*—The significance of such isolation has been recognized for many years, and in the writings of Darwin it is clear that the necessity of isolation was recognized, or at all events the value of such isolation was perceived. All the examples of divergence given by him tacitly implied such isolation although he did not clearly announce it, and he certainly did not recognize isolation as a necessity for the formation of a species. The difficulty which appealed to Darwin and others was to understand how isolation could have been brought about in so many hundreds of thousands of cases as would be needed to explain the origin of all species. The first and most natural method of isolation which suggests itself is geographical isolation. The isolation of animals on oceanic islands is readily understood. Moreover, it is easy to believe that migration of animals may occasionally lead a few individuals, or even a single pregnant female, to wander into a new territory where their offspring will have no mates except their own brothers and sisters. It is easy to imagine many changes in the earth's surface which have occurred during the evolution of organisms, and which may have separated small groups of organisms from their relatives and forced them to

live by themselves. Fishes in different rivers are isolated, and so are animals on the opposite sides of mountain ranges. Such geographical isolation has doubtless been frequent, and, where it has occurred, it has been beyond question a means of divergence of descent. This was pointed out as early as 1873 by Wagner, who erected upon the conception thus obtained a theory of evolution by isolation and migration, and insisted that all species must be traced to such a separation.

The theory of Wagner, however, was not received with much favor, for various reasons. Considering the hundreds of thousands of species of animals and plants, it is demanding too much to suppose that there has been such an extensive isolation of individuals as would be demanded by a theory which supposes that *all* species must have arisen from such geographical isolation. Moreover, we find, especially in the distribution of plants, thousands of instances where closely allied species actually occupy the same locality, and where, therefore, there is no possibility of geographical isolation, unless we make the unlikely assumption that they were once isolated but have later come together again. It is stated by some botanists that a majority of allied species will be found to occupy identical localities. Among higher animals different species are commonly separated by barriers, although we sometimes find them occupying the same locality. In the fossil snail shells, which have accumulated at the bottom of a lake of geological times, we find that there was a gradual change of species and a divergence of

character among snails occupying the waters of the lake where there could have been no question of geographical isolation. Such instances as these have made it impossible to look upon the theory of isolation advanced by Wagner as of more than subsidary importance.

But the fact that cross-breeding will prevent divergence and the impossibility of believing that natural selection acting upon averages could produce divergence have been constantly forced to the front. The great value of isolation in meeting these two obstacles to evolution has been so clear that others besides Wagner have been studying over the matter. In recent years the idea has been adopted by a new school of scientists that have perhaps added as much to the clearness of our knowledge of the method of evolution as any other students since Darwin. So long as *geographical* isolation was demanded as a necessary factor in the origin of species the idea could not be accepted. But it has now been pointed out that there are other factors of isolation which may separate groups of individuals from each other in such a way as to prevent cross-breeding. The conception of isolation by other means than geographical relations has occurred to several writers on evolution, but it has been most developed by Gulick and Romanes, and their names should be most intimately associated with the theory of isolation. Gulick in particular spent many years in careful study of animals in nature, and brought a fund of observations to substantiate his position. This is particularly interest-

ing since Gulick is a clergyman, and it is especially significant to find a clergyman making a lasting and valuable contribution to the doctrine of evolution. Romanes, by the clearness of his logic and the force of his fine mastery of English writing, has contributed an even greater share in bringing the new ideas to the attention of science.

In our study of the methods of isolation we must first notice that we may recognize two types of isolation. We may suppose, first, that the individuals of a species are separated into two groups without any reference to their characters. This would produce two groups which would be essentially alike. We may suppose, second, that the individuals are grouped according to some character in such a way that animals with a certain character would be grouped together, while others without it would be also grouped by themselves. In this case the two groups would be unlike at the start.

It is easy to understand that isolation of the second type would produce divergence of descent, for the two unlike groups would inevitably develop in different lines. But it is insisted also that the first type of isolation, the indiscriminate division into two similar groups, would also produce divergent descent, for the following reason: If one of the two groups should be large and the other small it could never happen that the average character of the one group should be exactly the same as the average character of the other. Indeed, it would be practically impossible to divide individuals into two groups of unequal size and have the average or

mean type of the two groups the same. Now, as we have seen, natural selection acts not on individual characters but upon averages. It is by raising or lowering the average that it advances the race. The two groups thus separated from each other, having of necessity a little different mean character at the start, would be differently acted upon by natural selection, even though they inhabited the same locality, and would develop in different directions. Such divergence could not occur before the isolation because of free inter-breeding which would keep the average of the whole race constant. But after isolation prevents the free crossing of the two groups, the slight differences in the average character would tend to increase, and divergent evolution would be the result. Hence it would follow that the simple fact of isolation would result in divergence of character, especially if the two groups were of unequal size. The smaller the group isolated from the parent stock, the greater the possibility of divergence, since the greater would be the probability that the average character would be different from the average of the race.

*Physiological.*—Recognizing, then, the great power of isolation, or "segregation" as it is sometimes called, to produce new species, we ask next what forces exist in nature which can produce such isolation. It will be best to notice first a factor upon which Romanes places the greatest stress, reserving until later the forces which Mr. Gulick brought to its aid. The force which Romanes placed foremost he called "physiological selection," a term that does not

well describe the factor concerned. The principle of physiological selection is that the primary isolation between individuals arises from differences in their reproductive powers. It is really sexual isolation.

It is well known that a breeder, by selecting his stock, can produce a very great variation from the original type, such as the fancy pigeons or the breeds of horses. It is a further fact that these varieties differ from true species solely in the fact that they can breed together, and that when allowed to breed together the varieties disappear as the result of cross-breeding. The breeder can retain them only so long as he prevents their cross-breeding. If left to themselves to return to a state of nature, all of the peculiar characters disappear as the result of cross-breeding. Now the variations which are thus produced affect almost every character of the birds except the power of cross-breeding. The fancier makes no attempt to select sterility, and his birds remain fertile with each other. If, however, there should arise among these different varieties a mutual infertility when crossed, they would at once be distinct species.

Artificial varieties are prevented from disappearing only by preventing inter-breeding by artificial means. Must we not assume then that natural varieties, in order to form species, have been prevented from inter-breeding by some natural means? It is a fact that natural species are commonly sterile when crossed. The step to physiological selection is then a simple one. The primal cause of isolation of individuals, says Romanes, is the appearance of

differences in the reproductive powers, such that a certain amount of mutual infertility arises among individuals. The reproductive powers of organisms are certainly variable, and if there should arise, among the members of a species, variations in the reproductive powers such that some individuals were infertile when crossed with the parent stock, but were fertile when crossed with each other, an isolation of the race into two completely separated groups would arise at once. The members of each group would be forced to breed with each other or not at all, and isolation would be produced although the two groups occupied exactly the same localities. Ordinary body characters may become very different and cross-breeding will eliminate them, but if there appear differences in the reproductive powers, associated with other differences, cross-breeding is at once checked. Isolation is produced, divergent evolution occurs, and new species will arise incapable of breeding together. Species are thus records of variations in the reproductive system.

That such a condition of mutual infertility would result in the origin of new species can hardly be questioned, but it is not so easy to see how such mutual infertility should occur. If the individuals with modified reproductive powers should be few, their chances of breeding together would be small. Such infertility would apparently result rather in extermination from inability to find proper mates than in the segregation of individuals. To suppose that large numbers of individuals varied in similar directions at once hardly helps us, for we cannot

understand why the reproductive powers should vary in the same way in many individuals simultanously. These lifficulties come chiefly from the consideration of higher animals. In lower animals and plants the reproductive process is very different. Among plants the fertilization is produced by pollen being carried to the stigma, and each stigma may receive pollen from many sources. Now it is well known that the time of maturing pollen and ovules is subject to much variation in the same species. Clearly those plants that mature their pollen early will be obliged to fertilize the ovules of plants that mature their ovules early, and in the same way the later plants must also breed together. This would produce an infertility between the plants from variations in the reproductive season. Again, it has long been recognized that the pollen of some plants has a greater power in fertilizing a certain sigma than has the pollen of other plants. A flower that is visited constantly by insects will receive many kinds of pollen, but among this pollen some grains have a prepotency over others. This prepotency may be slight or great. It may be so great that the prepotent pollen may fall upon the stigma quite a long time after the other pollen, and yet its action is so much stronger and quicker that it will itself fertilize the ovules before the less potent pollen has time to act, although, if the prepotent pollen had not reached the stigma, the other pollen would in time have produced the fertilization. A somewhat similar prepotency has been found among animals. It is certainly a fact that certain sports have sometimes

shown themselves so strong as to persist in spite of abundant opportunities for cross-breeding. In all such cases we have forces which would segregate groups. Those plants whose pollen has this prepotency would be almost sure to mate with plants for which they are adapted, and thus become isolated from others.

It is a question in these cases whether the mutual infertility is primary or secondary. Romanes believed it was the mutual infertility which arises first and produces the isolation. Others insist that the isolation is first produced by some other factor, and that mutual infertility aids; but the necessity of some kind of infertility to prevent the disappearance of varieties by crossing is everywhere recognized.

The significance of this idea of isolation has been greatly increased by the observations and considerations of Gulick, who has pointed out other factors which will tend to isolate individuals into groups so far as concerns breeding. The work of Gulick is especially valuable since it was the result of a long series of observations, and was not therefore simply a matter of hypothesis. Gulick gave many years' study to the land snails in the Sandwich Islands. These snails have little migrating power, many of them living in trees. He found that sections of the country very near each other, and having precisely identical characters, are inhabited by distinct species of snails. The amount of difference between the species was proportional to the distance of the localities from each other. Sometimes intermediate localities would show forms intermediate between

the types in extreme localities, and according to the usage of naturalists, the extreme forms would not be regarded as distinct species but only as varieties. But he called attention to the fact that he could make good species of them by simply burning the forests in the intermediate locality.

Such a peculiar distribution led him to inquire into its cause. According to the natural selection theory, the only explanation for the different species in these different localities would be that the conditions are different, and, therefore, that a different mean type had been best adapted to the different localities. But the conditions are so absolutely identical and the difference between the species is so plainly not connected with any difference in conditions, that Mr. Gulick found himself utterly unable to believe that each species was an adaptation to conditions brought about by natural selection. After a long study he concluded that the whole secret of the phenomenon is that the individuals in the different localities have been separated, or segregated, from their relatives, and have consequently been breeding together until each has departed from the original type in its *own* direction, and that the differences in the species are simply the result of such segregation and close breeding. This idea, once perceived, led him to a wider study of the conditions in nature which might have produced such segregation.

*Miscellaneous.*—We have not space to mention all of Gulick's factors, but enough must be outlined to show the general content of this principle of

isolation. In the first place he recognizes geographical isolation as an important factor, showing how the simple separation of individuals into groups would produce divergent evolution, because the average character of the groups could not be alike, and natural selection would consequently advance them in different directions. Secondly, he recognizes the factor of Romanes, and points out many conditions where the phenomenon of infertility will come into play. But besides these he finds other factors of segregation. The whole group of plants and many animals have little power of migration. Now such organisms will of necessity be obliged to breed with their neighbors. A plant in New York will of necessity cross with another in the vicinity and not with one in Iowa, even though the same species are found in the two States, and are not separated by barriers. If a species of plant is distributed over a wide territory it is certain that on the outer limits of the territory the number of individuals will be few, no matter how numerous they may be in the centre of the territory. Such individuals will not find their relatives so numerous as to make cross-breeding easy, and as a result the offspring of the same parents will be forced to breed together. Under such conditions it is evident that there is not a promiscuous breeding together of all individuals of the species, and, if the average character of the individuals on the outskirts of the territorial distribution is somewhat different from that in the centre, there will be a tendency to break up into two or more groups, from the simple fact that the

individuals are segregated, so far as concerns cross-breeding. The avergage character of individuals in Ohio will be likely to be different from that of the individuals in New York, and there will thus be a tendency to the production of two types from the fact that the individuals near each other will mate together.

Again, a different kind of segregation is presented by changes in habits. Suppose, for example, that some members of a species should try to escape their enemies by concealing themselves amid the stones, while others adopt a different method of escape; or suppose that some run up the mountains while others stay in the valley. It is evident that such habits would result in the breeding together of animals with similar habits. Or imagine some individuals acquiring a new food habit, feeding upon a new plant for example. Such a new habit would be almost sure to result in the breeding together of these animals to the exclusion of the rest of the species. This has actually occurred in the Colorado potato beetle, where some individuals of the species acquired the habit of feeding upon the cultivated potato. It is evident enough that these individuals thereafter breed together, to the exclusion of other members of the same species that may not have adopted this new plant food. If other individuals do not happen to adopt this new habit, it is certain that they will not cross to any extent with those feeding on the potato, and such a change of habit has thus produced a division of the species into two groups. Two species of rats in the Solomon Isles

are believed to have thus arisen, one group acquiring arboreal habits and the other remaining on the ground. A race of deaf-mutes is arising by the habit of associating deaf persons in asylums. One need only to look at the social life of a city to see how effectually social habits separate mankind into groups which are isolated from each other, so far as reproduction is concerned.

Another factor leading in the same direction is the social instinct of animals. This unites into bands individuals with like habits, and thus, commonly, individuals with like ancestry. A herd of antelopes is largely made up of children of the same male parent, at least in small herds where there is only one male. A colony of insects has only one female parent. Social instincts, wherever they occur, tend to group together individuals which have like characters, since they have like ancestry. Of course such association is frequently broken down, but it nevertheless represents a force which tends to group individuals together.

Isolation would also be produced by protective coloring. Suppose, among grasshoppers there is a variation in color, some being green and others brown. The green individuals would be protected in the grass from the fact that their color would hide them from the detection of birds. The brown individuals would in a similar manner be protected on the sand. Thus in time only green animals would be found in the grass and brown ones on the sand, and the inevitable result would be the mating together of animals of similar colors. Moreover,

there seems to be frequently shown a preference on the part of animals for others with special color marks, sometimes called "recognition marks." These marks would thus tend to segregate together individuals with certain markings, and would explain the utility of markings otherwise unintelligible.

It is even claimed by the advocates of the isolation theory that natural selection itself is only one method of isolation. By the extermination of the least fit the fittest are left to breed together unchecked by cross-breeding. It is really the isolation of animals with like adaptive characters which produces the new type, and natural selection thus only serves as a means of producing isolation and preventing cross-breeding.

Without going further into details these illustrations will be sufficient to indicate the nature of this principle of isolation. The essence of this new attempt to reach an understanding of the origin of species and remove the difficulties that have been raised to the theory of Darwin, is by showing that there are in nature many forces which have a tendency to separate into groups individuals of like characters. By breeding together of such individuals the swamping effects of cross-breeding are avoided and the difficulty of understanding divergent evolution is largely removed.

### *Relation of Isolation to Natural Selection*

It remains to consider the relation of this factor of isolation to the other forces which have contributed to the origin of species. It is necessary, in

the first place, to avoid being confused by the personal discussion of the adherents of the different theories. Some of the Neo-Darwinians are so satisfied with the theory of natural selection as an entire theory that they either accept nothing new, or, if they do, regard it simply as a part of their own theory of natural selection. Isolation they accept as a factor in nature, but regard it simply as a part of natural selection. At the other extreme, Romanes has claimed that the three forces contributing to the origin of species are Variation, Heredity, and Isolation. Granted that variation and heredity exist, then the problem of evolution is simply the study of the causes which have led to isolation, natural selection being simply one means of isolation. Not a little of the discussion which has arisen over the theory of isolation has been on the point whether it is to be regarded as a part of the general theory of natural selection, or whether natural selection is a part of the theory of isolation. Such verbal questions are of no significance to our purpose, for we are trying to find out what we actually know to-day as to the method of the origin of species, and not whether Darwin or Wallace or Romanes or Weismann or any other one happened to hit nearest to the truth. If we leave this question out of account we come to a uniform recognition, by all schools of evolution, that isolation must have been a very important agent, well-nigh universal, in the origin of species by divergence.

But the question, whether isolation starts the divergence, or divergence starts the isolation, is one

which is fundamental and represents a real difference of view. Before groups of like individuals can arise, there must appear among them some character upon which the isolation can be based. Until there has been produced some differences among individuals, it is clear that it is impossible for different groups to be formed, based upon distinct characters. Thus it is said that divergence must precede isolation instead of being the cause of it. Even if this be true, it does not in the least affect the belief in the great efficiency of isolation in producing divergent evolution, for without such isolation the different characters would soon disappear by cross-breeding. Changes in habit and structure certainly do appear, although we may not understand their cause. If we can, by means of the factors above outlined, understand how such varieties may be brought to mate together instead of crossing promiscuously with the parent type, we have at once advanced our understanding of the process very greatly, and have silenced some of the most serious criticisms which have been raised against the theories advanced by Darwin.

But the advocates of the isolation theories insist that isolation will in itself be the cause of divergence. As already pointed out, the simple separation of individuals into two groups will result in divergence, from the fact that the average character of the two can not be the same, especially if one group be small; and then close inter-breeding will increase the differences in character, and thus produce divergence. It is only by such divergence, produced by

isolation, that we can understand the origin of several species, closely allied to each other, in the same locality, and this condition appears to be a very common one, at least among plants. It is only by denying that two species can arise in the same locality that the critics of the doctrine of isolation can question the conclusion that isolation is in itself a primary cause of divergence. Leaving out of account, however, such polemics, there need be no dispute over the matter. Whether isolation be really included in natural selection or not, it was certainly not recognized by Darwin as of such importance as it appears to be to naturalists to-day.

Whether isolation deserves to be regarded as one of a great "tripod"—Variation, Heredity, and Isolation—and whether natural selection is to be regarded as one type of isolation, may well be questioned. But the unquestionable conclusion must be that natural selection has been an important factor in the development of species, and that the various forces above mentioned which produce the separation of groups from each other in such a way that free inter-crossing is prevented, have doubtless been a common, if not a universal and necessary factor, in the divergence of species from common centres. This isolation and segregation aids us greatly in understanding how the laws of reproduction have produced a variety in nature, or, as it is termed, *polytypic* evolution. Just how widely these forces have been in action, and just how far natural selection alone may account for our present species, may for a long time be unsettled. But we may be sure

that the many forces pointed out in this section by which individuals are grouped together, so far as breeding is concerned, have been important factors in the origin of species, and their recognition has removed some of the serious difficulties which stood in the way of understanding natural selection when no such forces were recognized or were only dimly understood. Whether Darwin recognized them or not, or whether they are included in Darwinism, are questions of no special importance, for it is certain that neither Darwin nor his followers perceived their great significance until they were pointed out in somewhat recent years by Gulick and Romanes. We must therefore recognize these theories of isolation and segregation as actual contributions to our knowledge of the origin of species, and as doing more toward clearing up our ideas of the method of evolution than any one contribution since Darwin. The theory of natural selection demands the additional theory of isolation, to enable it to produce divergence.

### *Organic Selection*

One of the most recent contributions to the method of evolution has the merit of having been conceived independently by three different naturalists, and recognized from the first as a factor of significance by prominent advocates of both the Neo-Darwinian and Neo-Lamarckian school. It has been called *organic selection*. The sources from which this idea sprung were quite different, its

authors being, one a psychologist, one a paleontologist, and the third a naturalist who has made a special study of instincts. From such different standpoints the arguments that have led to the theory have been somewhat varied. In general it may be said that these naturalists came to this theory because they felt the inadequacy of natural selection, as previously understood, to account for all the facts, and because they felt that the Lamarckian factor is at least doubtful, and, even if true, is perhaps not sufficient to meet the demands made upon it. The theory of organic selection is, in a sense, a compromise between the views of the two chief schools. With Neo-Darwinism it abandons the inheritance of acquired characters, but with Neo-Lamarckism it puts the influence of acquired characters foremost in guiding the course of evolution.

### *Ontogenetic Variations*

In the first place a sharper contrast than ever is drawn between such variations as result from heredity and those which arise from the direct action of the environment upon the individual. This is, of course, simply the difference between congenital and acquired variations, but the latter are now regarded as forming a much larger share in the make-up of an individual than has previously been supposed. The life of the individual may be supposed to begin at the time of the fertilization of the egg. By this time all the hereditary traits that he is to receive are already combined in the egg,

*i. e.*, all his congenital characters are within him. But from this moment there begin to act upon him the direct influences of the environment, and all subsequently developed variations are acquired rather than congenital. They are frequently called *ontogenetic variations*, which is a better term than acquired, since all variations must of course be acquired at some time, and the term ontogenetic indicates that they are acquired by the individual and not by the germinal substance. These ontogenetic variations are entirely independent of those which arise in the germ plasm, since they are supposed to affect the body simply and are perhaps not transmitted by heredity. But such variations have a very great influence upon the individual. From the very beginning of his life he is influenced by them, and the characters that he has when adult are a combination of some that he has received by inheritance with some which he has developed himself as the direct result of the action of the environment upon him. Since these latter characters are the result of the action of the environment, they are commonly adapted to it. To be sure, as elsewhere pointed out, we do not understand how environment can act upon the individual in such a way as to produce even acquired adaptive changes in it. Why a muscle grows with use or diminishes with disuse, why sensations become more acute when exercised, why changes in food or climate modify colors, why the shapes of leaves and the length of the beaks of birds change with climate, we have not the faintest notion. But such adaptive changes do appear

during the life of the individual. They form the basis of the Lamarckian theories and are patent in every-day life.

It is impossible to determine at present to what extent the characters of an adult are inherited or congenital, and to what extent they are readily developed by each individual independent of inheritance. When we remember what extensive changes can be produced in an organism by changes in its environment, and remember that the individual from the outset is acted upon by the environment, it would seem to follow that its adult characters must in no inconsiderable degree be simply acquired rather than congenital. But it is difficult or impossible to distinguish the two classes. In the studies of variations which have hitherto been made there has been no attempt to distinguish between them. When it is found that the length of the beaks of birds varies widely with climate, or that the length of the wings or legs shows variations on either side of a mean, it has been assumed that these are innate differences, and therefore, if selected, are matters of heredity. Most of the significance attached to the statistical study of variation mentioned in an earlier chapter depends upon this assumption. But it is at least as probable that the variations are simply due to the action of the environment, habit, or use, and hence purely acquired. Most of the studies of variation which have been made, up to the present, have consisted in recording variations, either great or small, but without any attempt to determine to what extent they are really congenital, and to what

extent due to the action of the environment upon the individual. Considering the great difference in the relation of the two classes to the problem of evolution, it is evident that no very clear results will be reached until the two types of variation are more carefully separated.

Be this as it may, it is certain that the environment has a considerable influence upon the development of each individual, independent of his inherited characters. It is equally evident that these acquired characters must change with every change of condition or habit. If an animal acquires a new food plant or a new habitat, if he learns a new method of protecting himself, or if a plant starts to grow in a soil different from that in which it has hitherto lived, these changes will, of course, produce their effect, and acquired variations will result. Now, as we have seen, it is difficult to believe that these variations will so affect the germ plasm as to be transmitted to the next generation, but it is equally clear that if the next generation should be placed under the same conditions it would independently develop similar variations, entirely independent of heredity. So long as the environment remains the same, each generation will develop, after its birth as an individual, the same sort of acquired variations. These, appearing regularly in subsequent generations, would probably be regarded as inherited, although in reality they are only independently acquired by each individual. They would not be a part of the inherited nature, but only the result of the "nurture" to which each individual is subjected.

### *Agency of Acquired Variations in Guiding Natural Selection*

The essence of the theory of organic selection is, that these acquired variations will keep the individuals in harmony with their environment, and preserve them under new conditions, until some congenital variation happens to appear of a proper adaptive character. The significance of this conception is perhaps not evident at a glance. It may be made clear by considering, for illustration, the problem of the development of habits and organs adapted to each other. It is impossible to believe that an organ develops before the habit of using it, for if it did it would be useless. On the other hand, the habit of using an organ could not arise before the organ makes its appearance. We must thus believe that the organs and the habit of their use appear together, a very difficult or impossible conception for hap-hazard variation. Now organic selection tries to show that the adoption of a new habit by an animal will result in the development of structures adapted to the habit, but by a principle that does not involve the inheritance of acquired variations. Assuming that some changes in conditions caused certain animals to adopt a new habit, Weismann's theory would force us to believe that some structural changes would follow, from variations in the germ plasm, which would be parallel to the acquired variations developed by the new habit. But when we conceive, as Weismann must, that congenital variations are indefinite and in all directions, it becomes a matter of infinite improbability to suppose

that just the right sort of variations will follow such a change in habit at just the right moment. The Lamarckians, finding that habit and structure follow each other so closely, have felt obliged to assume that the one produces the other, while of course the Weismannians must deny such a conclusion.

If it were not necessary to assume that a congenital variation appropriate to the habit should follow *immediately* when the habit changes, this difficulty would be greatly lessened. It may be admitted that it is so improbable as to be inconceivable that a new habit should be followed immediately by a congenital change in structure appropriate to the new habit, unless there be some inheritance of acquired variations. But it is quite probable, even upon the principle of hap-hazard variations in all directions, that some such congenital variation might appear in course of time. If the individuals could be kept in their new habit long enough, it would be pretty sure that eventually some congenital variation would appear of an appropriate character. Now the acquired characters will serve to preserve the individual in the new conditions. When an animal adopts a new habit its body begins to change at once, and he soon acquires a development of muscles and bones adapted to his new habit. He may, indeed, not transmit these characters, and his offspring may be at birth no better off than he was at birth. Each generation acquires these characters for itself so long as the conditions remain the same. But the new characters, even though not congenital, adapt the individual to its new conditions and enable

him to live successfully in these conditions. These individuals are therefore able to contend successfully in the struggle for existence, their acquired characters being just as useful to them as they would have been if congenital. This is repeated, generation after generation, similar acquired characters being redeveloped by each generation.

Remembering then the great numbers of variations that are constantly occurring as the result of modifications of the germ plasm, it is probable, indeed certain, that after a time some congenital variation will appear which will be of direct use to the animals in their new habits. During all this time the majority of variations will appear and as quickly disappear, since, being of no special use, there will be nothing to preserve them, and cross-breeding will soon eliminate them. But when, perhaps after hundreds of generations, there does appear a congenital variation which aids the animal in its new habit,—an old habit by this time,—such variations will be selected and become a part of the inheritance of the race. The individuals with these congenital variations will, from the outset, have an advantage over others, since the congenital variations will enable them to adapt themselves more closely to the conditions than would purely acquired characters. Thus the acquired characters keep the individuals alive until the proper congenital variations appear, and the new habit actually determines what sort of congenital variations shall be preserved, and guides the process of evolution.

Perhaps a concrete case may make this somewhat

obscure theory a little clearer. Imagine, for example, that some change in conditions forced an early monkey-like animal that lived on the ground, to escape from its enemies by climbing trees. This arboreal habit was so useful to him that he continued it during his life, and his offspring, being from birth kept in the trees, acquired the same habit. Now it would be sure to follow that the new method of using their muscles would soon adapt them more closely to the duty of climbing. Changes in the development of different parts of the body would inevitably occur as the direct result of the new environment, and they would all be acquired characters. The children would develop the same muscles, tendons, and bones, since they, too, lived in the trees and had the same influences acting upon them. Such acquired characters would enable the animals to live in the trees, and would thus determine which individuals should survive in the struggle for existence, for these modified individuals would clearly have the advantage over those that stayed on the ground, or did not become properly adapted to arboreal life by acquired habits. All this would take place without any necessity for a congenital variation or the inheritance of any character which especially adapted the monkey for life in the trees.

But, in the monkeys thus preserved, congenital variations would be ever appearing in all directions. It would be sure to follow that after a time there might be some congenital variation that affected the shape of the hands and feet. These would not be produced as the result of the use of the organs or as

acquired variations, but simply from variations in the germ plasm. There might be thousands of other variations in other parts of the body in the meantime. The miscellaneous variations, however, would not persist. But as soon as variations appeared which affected the shape of the hands and feet, the fact that the animal had continued to climb trees would make these variations of value, and therefore subject to natural selection. Selection would follow, and thus in time the monkeys might be expected to inherit hands and feet well adapted for climbing. The acquired variations, in such a case, had nothing to do with *producing* the changes directly, but they did shield the animal from destruction until congenital variations appeared. Acquired variations have determined that the individuals shall live in trees, and this life has determined what congenital variations will be preserved. Indirectly, therefore, the acquired variations guide evolution.

This factor would also aid in explaining the origin of co-ordinated structures, which have been always a puzzle to natural selection. How, for example, can we imagine that chance congenital variation shall *at the same time* cause an increase in the size of the deer's horns and in the strength of his neck and shoulders? Either without the other could not exist. But we can imagine that some congenital variation increased the size of the antlers, and then clearly enough acquired characters would of necessity increase the size of the neck and shoulder muscles, thus enabling the animal to carry the large

antlers. This might continue many generations. Eventually another series of variations of a congenital character might affect these muscles. These would be at once selected, if they enabled the animal to carry its antlers more easily, and thus in time neck and antlers would be co-ordinated to each other. The animal by acquired characters adapts itself to its conditions and waits until a proper congenital character appears. A combination of characters to make a co-ordinated system of organs is thus made possible, in a manner that natural selection alone is unable to account for.

### *Consciousness a Factor*

This conception of the action of selection evidently makes consciousness a factor in evolution. It has always been claimed by the Lamarckian school that consciousness aids in the process of descent. It has sometimes been supposed that by this claim is meant that by conscious efforts an animal can modify its structure; but such a conception has certainly not been held by scientists in recent years. Consciousness may, however, lead to the use of organs or to the adoption of new habits, and, if the view we are now considering be sound, such use of organs, or such habits, leads to the development of acquired characters which enable the individual to live in new conditions more successfully, until after a time congenital variations take their place. Consciousness thus becomes an indirect factor in evolution. Indeed, the attempt is sometimes made to

extend this principle of consciousness to all organic life, and to find even among the lower plants something which corresponds to it. Such an expansion of consciousness is, however, too crude and unintelligible to take its place in our general conception of nature. But, if organic evolution be a factor, consciousness becomes a force of considerable importance among higher animals. Moreover, this is just where there appears to be the greatest need for some aid to natural selection. As we have already seen there is strong evidence for the inheritance of acquired characters among plants, so strong indeed that some botanists insist that it is a matter of demonstration that such characters are inherited. Among animals, however, there is little evidence for such inheritance and apparently a growing disinclination to believe in it. Thus it is seen that the factor of consciousness would come into play just where acquired characters become of most doubtful value. Among plants, because of the wide distribution of the germ plasm through the body, there is less difficulty in accepting the inheritance of acquired characters, and here consciousness is not needed. Among animals where the inheritance of acquired characters is more doubtful, to say the least, this factor of consciousness takes its place.

### *Organic Selection and Natural Selection*

It has been said that organic selection is a sort of compromise between Weismannism and Lamarckism. It can, however, hardly be called a compro-

mise. It abandons entirely the Lamarckian position of the inheritance of acquired characters, and that such agencies as use and disuse have any direct influence in producing variations which modify the offspring by inheritance. The only Lamarckian feature that is left is, that the environment, through the acquired characters it produces, does have an important influence in guiding evolution. Such a position is, however, perfectly in accordance with Weismannism, as is shown by the fact that organic selection is endorsed by Weismann. At the same time, there is no doubt that it quite materially alters the earlier notions of natural selection and presents that theory in quite a different aspect. For it is plain that with this idea the guiding force in evolution is no longer simply the natural selection of minute, hap-hazard variations, as Darwin supposed, but a combined action of the indirect influence of acquired variations and the selection of hap-hazard congenital variations. It has long been felt that the theory of evolution by the selection of mere hap-hazard variations presents great difficulties, and, if it were possible to find some more distinctively guiding force the gravest difficulties of natural selection would disappear. It is for this reason that the Lamarckians insist upon acquired variations as a guiding force, and others claim that variations occur along definite lines. This new factor of organic selection tries to show that acquired variations, although not directly inherited, do furnish such a guiding force, since they preserve the life of the individual by adapting him to his new conditions, until

a time, after many generations perhaps, when some congenital variations of a proper character appear.

As to the value of this newly conceived factor in evolution, it is perhaps too early to determine. Of course it fails to explain why congenital variation appears in an animal, adapting it to the condition of life it has assumed. It still depends upon *chance*, only it gives more time during which the animal may wait for the congenital variation to appear. It fails to explain why, after the first favorable variation in the right direction, others should follow in the same direction without waiting long generations. In the end, organic variation must depend upon the selection of chance variations, for it offers no explanation for any force guiding the appearance of inherited variations. The value of Lamarckism is in the fact that, if it be accepted as a factor, it explains how variations happen to be of a favorable character. It finds a causal relation between the action of the environment and the acquired variations which are produced, leading us to *expect* that the variations should be useful. Organic selection lacks this element of strength, for, like Weismannism, it must depend upon hap-hazard variation, produced, perhaps, by changes in the environment or by sexual union, but having no direct relation to external conditions. Organic selection simply extends the process over a longer period, and makes it more probable that the proper variations should arise in time to be of use.

If this factor of organic selection is admitted as a force, we must ask how wide is its application. Is

it a force like natural selection that will apply everywhere, or is it confined, as are the effects of use and disuse, to certain organisms? In answer to this it is apparent that its influence will be more extended than the action of use and disuse, and more extended than the limits of consciousness. Wherever acquired variations occur organic selection will apply. Wherever environment, either food, climate, or conscious action, produces direct modifications of the body of animal or plant, these acquired variations will aid in preserving the individual until the proper congenital variations appear. Organic selection would therefore seem to apply wherever the environment produces a direct adaptive variation in the body of the individual.

In thus basing evolution upon acquired variations we seem to have placed it upon a firm foundation, for acquired variations are very tangible things. We feel that we understand them much better than congenital variations. But, if we pursue the inquiry further, we shall find that we are not much better off, so far as concerns an understanding of the real life processes, when we consider the one set of characters than when we consider the other. It is really no easier to explain an acquired character than a congenital character. We know that a muscle increases with use and that the skin tans with exposure to the tropical sun, and, on the other hand, we know that some individuals are born with extra toes. But we understand the one series of facts scarcely better than the other. We have felt it necessary to find some cause for variations appearing where needed,

and variations adapted to conditions. The Lamarckian finds this cause in the adaptations which every organism makes to meet its surroundings. But we are then confronted with the demand for an explanation of how the environment produces such a result upon the individual, a question wholly independent of inheritance. Why should the change in the environment produce variations in the individual which fits him for his surroundings, rather than changes that are of a disadvantage to him? Why should the use of the head in butting, for example, produce the growth of the bones into horns? The only answer to such questions is to retreat into the properties of living matter. It is the nature of living matter to adjust itself to its environment. But with such a statement we have of course retired into the region of the unknown, and have hardly advanced ourselves at all in the attempt to understand life. A theory that bases evolution upon acquired characters, just as truly as one that bases it upon congenital characters, must retreat into the impregnable position of the unknown properties of life adjustment. So far then as concerns the real understanding of evolution, it makes little difference whether we admit the inheritance of acquired characters or not. We do not understand them any better than we do congenital characters.

It is, however, a fact of observation that acquired variations *are* adaptive, and to this extent they may aid in the problem if they are inherited or if they have the influence assumed in the theory of organic selection. But there are some classes of facts that are

not amenable to this theory. For example the use of the teeth actually wears them away. They are not, like the muscles, increased by use, but *decreased*, especially at points where the wear is the greatest. But one of the most striking series of facts disclosed by the studies of recent years has been the gradual development of teeth among the vertebrates. It has been shown by a most exhaustive study that the tubercles in the teeth, as they appear in successive vertebrates always arise where the action of the teeth in chewing brings the greatest use. This change has been followed in a large number of types and in all directions the development of the teeth has been of a similar nature, viz., the appearance, in later types, of tubercles at regions where the greatest strain came in earlier ages. But we find that acquired variations do not produce tubercles where there is the greatest wear, but rather flatten the tooth or cause depressions. Acquired variations do not then explain the appearance of tubercles at places of greatest wear. Nor can organic selection be of any more value here. The acquired variations produced by the wear of the teeth decrease rather than increase their efficiency and, therefore, *cannot* serve to keep the individuals alive until the proper congenital variations arise. We can only retain the theory here by making the supposition that the use of the young tooth, while it is still growing and before it has reached its permanent adult condition, may produce the development of tubercles, just as use produces greater growth of muscles. For this supposition there is as yet no confirmation, and

organic selection, as well as Lamarckism, fails to reach such cases.

Organic selection must undoubtedly be regarded as a factor in the evolution of species. This is granted on all sides. In the study of the history of man it becomes of extreme significance, but this subject cannot be considered in this work. Whether this new factor can be considered as contributing so much to the problem as to overcome the obstacles which have been found in the way of Lamarckism and Weismannism, is at least very doubtful. It is a factor which throws light in certain places but not everywhere.

*Weismann's Germinal Selection Theory*

Finally we must refer to one further theory of Professor Weismann, which endeavors to meet the difficulties raised against his earlier doctrine that bases evolution upon the selection of congenital variations only. In considering this theory, we are once more taken into the region of pure speculation. It would be hardly worth our while to refer to it were it not for the fact that it implies a new realm of variation among organisms, and is in this respect at least suggestive. At the outset, we must notice again, that, in attempting to build up evolution of species by known forces, the weak point in the chain has been variation. That variations exist is patent enough, but what causes them is still uncertain. The mixture of germ plasms furnishes a cause, but an insufficient one. The effect of changes in the

environment may furnish a cause, but this is uncertain. Why similar variations appear in many individuals at once, why they should involve whole groups of organs at the same time, why they appear when and where needed, why they follow along definite lines for long periods of time, all these questions remain unanswered. It is to meet some of these difficulties that Weismann has devised a new theory.

He begins by frankly acknowledging the difficulties standing in the way of natural selection as conceived by Neo-Darwinians. He speaks of the flood of objections raised against the theory of selection, touching its ability to modify many parts at once. He recognizes that the summation of accidental variations is insufficient for the transformation of species, admitting that, if each generation should be obliged to wait for a chance variation before it could advance along a given line, evolution would never get anywhere. He sees thus a necessity of finding something to account for "determinate" variations. He sees that the force of the difficulties is becoming so great as to drive some of the younger naturalists to abandon natural selection entirely as a causative force, claiming that to ask its acceptance demands us to "abrogate reason." While of course Weismann does not admit the justice of the abandonment of natural selection, he does feel that it is necessary to find some support for it at its weak points or it is in danger of being abandoned altogether. Now such an admission appears to be too sweeping, for natural selection, in spite of its weak-

ness at some points, still stands as the most universally acting factor yet discovered regulating the origin of species. It is especially suggestive to find that such damaging admissions are made by Weismann, who has been the leading advocate of natural selection in recent years and has led the progress toward the abandonment of Lamarckism. In reading these admissions on his part one is inclined to believe that he has made them in order to pave the way for the new theory which he advances to the aid of natural selection. Be this as it may, his present attitude toward the problem is as follows:

The one great need for the support of the selection theory is something to account for the occurrence of variations when needed which will be of a useful character. If it is possible to explain the appearance of simultaneous variations in many individuals, of useful variations when they are needed, then we shall have no further difficulty in understanding the action of natural selection. In answer to this demand Weismann extends the principle of selection to the parts of the germ plasm. Earlier, Professor Roux has suggested that we can look upon the *cells* of which an organism is composed as having a struggle with each other. Each cell must feed and grow as well as multiply. The amount of food and space in the body is limited, and those cells which are best equipped will obtain food and drive the others out of existence. In the growth of the body, therefore, useful qualities appearing in the cells will be preserved, and the adult will be made up of cells selected by this process. This idea is of course simply

natural selection applied to the cells in the individual, instead of applied to individuals.

Now Weismann uses the same principle, only he carries it over to the realm of his germ plasm. The whole matter is pure hypothesis and would hardly have received any attention if it had not come from Weismann. He has tried to picture the internal structure of the germ plasm. The structure is, of course, far below the reach of the microscope and must be built up entirely by the imagination. There is no reason, therefore, for believing that the structure imagined by Weismann represents anything more than imagination. But it serves him as a basis for an attempt to explain variation. He supposes the germ plasm is made up of ultimate elements which are combined into groups, and these groups into others of a second order. To each group he has given names (*biophores*, *determinants*, *ids*, *idants*). With all this we need not trouble ourselves. He supposes further that certain of these groups, which he calls determinants, control the development of definite organs; one determinant, for example, controlling the development of the middle toe of the foot, and others controlling the development of the other toes, while a more complicated group controls the development of the leg as a whole. Now, in accordance as these special groups are vigorous or weak, the organ which they develop will be strong or weak, the character of the determinant regulating the character of the organ as the animal grows to maturity. But the germ plasm in the reproductive organs is increasing in amount

by growth and for this reason it demands food. Each determinant Weismann looks upon as independent and demanding food in order to grow properly. He tell us that there is a struggle among these determinants for food, just as between the different cells of the body or the different individuals of a species. The strongest determinant gets the most food. If they are of equal vigor each will get a proper share of the food supply, and all will develop equally. In this struggle among the germ determinants Weismann thinks he can explain the appearance of variations in definite lines. Imagine, for example, that as the result of some mixture of germ plasm, there arises an egg with the determinant of the middle toe a little more vigorous than those of the other four toes. Such an egg would, of course, develop into an individual with an enlarged middle toe, which individual, if the middle toe be of an advantage, would be preserved by natural selection and would produce offspring. In this there is nothing especially new. But Weismann goes on to say that, while the reproductive bodies of the next generation are developing, the determinant of the middle toe has from the start an advantage in being more vigorous, and in its struggle with the other toe determinants it will gain more than its share of food. This will result in its growing in size at the expense of the other four determinants. If, therefore, we imagine this struggle to go on during the development of the individual, it will follow that by the time the next egg is ready for development, the middle-toe determinant will have

distanced its competitors and become even more vigorous than at first. As a result the next generation will have a middle toe larger than the present generation, while the outer toes will be still smaller. In other words, the next generation will show the peculiarity of the first generation still farther developed. But the same struggle continues in the next generation, the middle-toe determinant having an even greater advantage over the others. Thus, just as soon as one toe determinant becomes slightly more vigorous than its rivals, we may expect in successive generations to find the character in question becoming more and more strongly marked. Of course, if this peculiarity should be of disadvantage to the individuals they would be eliminated by natural selection, while if it be of advantage they will be protected by the same force. As long, therefore, as the peculiarity continues to be of advantage it may be expected to continue to increase, generation after generation. Thus natural selection of individuals would not need to wait for a chance variation to make its appearance, and then wait another long series of years for a second to appear in the same direction. Variations will tend to appear in successive generations along definite lines, and, with natural selection to preserve the individuals now and then, the process of evolution will follow definite lines for long series of years.

Here, then, is a method of meeting one of the most serious difficulties in the way of natural selection. It may be supposed that natural selection does preserve a chance favorable variation. But

after this one step has been taken, in accordance with the natural selection theory alone, there must be a long pause before another variation in the same direction arises, for if variations are fortuitous they would occur in all directions, and would not likely appear in the same line in successive generations. After having preserved the first step toward the increased middle toe, for example, it might be required to wait for quite a long time before another variation of the same sort appeared of sufficient value to be preserved by natural selection. Meantime, other variations in other directions might occur to interfere with the whole process. But here, in this new suggestion of Weismann, the needed variations will follow each other rapidly. The selection of the first step in the proper direction would preserve individuals in whose germ plasm the middle-toe determinant had an advantage from the outset, an advantage which would be increased as the result of the struggle among the germ determinants for food. Once the line was started it would follow in the same direction, generation after generation. Natural selection of individuals would start the process, but *germinal selection*, as Weismann calls it, would continue and augment it. Here we find an explanation why following generations should vary in the same direction. This suggestion further offers an explanation of the appearance of many adapted variations occurring together. It might be, for example, that it was not simply the determinant of the middle toe which had an advantage over the other toes, but that the

determinant that controlled the whole leg and arm was more vigorous than those that controlled other parts of the body. This would produce corresponding variations in the whole appendage, and successive generations would see the legs and arms undergoing successive modifications in definite directions. Here, too, we find an explanation of the disappearance of organs which are not needed. In cave animals, for example, the determinants which direct the development of the eyes might be outstripped in the struggle with their rivals that controlled the development of the other sense organs. Natural selection would of course preserve those individuals that had their other senses especially well developed, and in successive generations the eye determinants would be crowded out of existence by the others, and the eyes would correspondingly disappear. In short, Weismann thinks that this new idea furnishes exactly the necessary force needed to control variations and to explain variation in definite lines and where needed.

Weismann regards this theory as simply a further application of natural selection. He says that hitherto we have confined this law to the selection of individuals. Roux extends it to the selection of the body cells, suggesting that the development of the body from the egg is influenced by the selection of the most vigorous cells at the expense of the least vigorous. Weismann now extends it to the selection of the different units in the germ plasm. In so doing he makes selection influence the following generations and thus appear as congenital

variations, furnishing thus the material for natural selection of individuals to act upon. The whole problem of evolution is thus one of selection. The selection of the germ determinants regulates the congenital variations of the following generations. The selection of the body cells regulates the development of the individual from the egg, and the selection of individuals determines which of the types shall remain to continue the process in the following years.

### *Criticism of Germinal Selection*

This theory needs only brief notice. In the first place it is questionable whether it can properly be called an extension of the doctrine of natural selection. Natural selection is the result of a struggle resulting from over-production. It results in the elimination without offspring of those lines of descent that do not meet the conditions. Extermination of the unfit is its essence. This new idea of germinal selection is not based upon over-production, nor are the unfit determinants exterminated. There is, therefore, no selection in the sense in which that word is used in the term "natural selection." Germinal selection is simply increased vigor resulting from good or poor food supply.

But of course the primal criticism of this new theory is that it is wholly imaginary, and for it not a single bit of evidence can be produced; nor, indeed, does it seem probable that it will ever be possible to adduce evidence for it. There is no evidence

that the germ substance is thus divided into groups, no evidence that determinants, in Weismnn's sense, exist. There is no evidence that such determinants, if they do exist, have any struggles with each other. The whole conception is, from beginning to end, based upon purely imaginary suppositions, is pure hypothesis with no support in substantiated facts. Weismann, by the use of imagination, has built up an ingenious structure for his germ plasm, and then imagined that the parts of this imaginary structure act in certain ways. Of course no one can accept seriously such a purely imaginary structure, and we can hardly believe that Weismann has contributed anything to the problem of the solution of the origin of species by such a long series of purely imaginary suppositions.

We cannot, indeed, place much confidence upon speculations that deal in "plasms." It must be noticed, however, that Weismann is not the only biologist who has attempted to construct the imaginary architecture of protoplasm and germ plasm, for several others have undertaken the same task. It is claimed that such attempts are justified by the atomic theory of chemists. Chemists have never seen atoms nor molecules, but the world recognizes the cogency of the atomic theory. So, in biology, we may be obliged to recognize ultimate units and perhaps build up some imaginary structure of protoplasm which corresponds to the formulæ built in the imagination of the chemists. Now, while this may be true, it is certain that the subject has not progressed as yet sufficiently to demand more than passing

interest. The atomic theory certainly receives wide verification from observation and experiment. The theories of the architecture of germ plasm have not yet received any verification. They exist simply in the minds of the biologists. Moreover, even from the standpoint of pure hypothesis, Weismann's theories have been severely criticised. Weismann's own students regard his theory as untenable in many respects, since they find it contradicted by observation. Weismann's germ-plasm structure has had most of its foundation stones pulled from under it in the few years' study to which it has been subjected.

At all events, it must be acknowledged that we have not advanced far in the explanation of the origin of species if we are obliged to base our explanation upon purely imaginary properties of purely imaginary units of life. If this theory of germinal selection could only be shown to represent a truth, it would apparently be of very decided value in explaining variation along definite lines, and thus meeting some of the most serious difficulties offered to the earlier conceptions of natural selection. As matters stand to-day, we can only say that the value of the theory is simply in the suggestion that nourishment of any part of the germ plasm, by increasing its vigor and depriving its neighbor of proper nourishment, may tend to produce cumulative effects in subsequent generations. If we consider the nourishment of any part of the body to affect subsequent generations, we should have the inheritance of acquired variations with its difficulties.

Weismann avoids this conclusion, which he thinks inconceivable, by supposing that the effect is produced by the nourishment, not of the part of the body, but of the germ plasm that controls the development of the next generations. This has nothing to do with the use of the organ by the individual, but simply with the relation of the struggling parts of the germ plasm to each other, and the results may or may not be parallel to the effects of use and disuse. But the whole subject is too imaginary to give us any feeling that we have grasped any new truth with the formulation of such a hypothesis. If in the future we do succeed in building up an architecture of the germ plasm with as much foundation as that which exists for the architecture of the chemical molecule, doubtless new truths will be disclosed. But such a structure must come as a result of the study of the facts of nature and not by a pure effort of the imagination.

## *Summary*

The supplemental theories outlined in this chapter in aid of natural selection are each calculated to meet a different class of difficulties which, as we have seen, have become somewhat serious. The theory of isolation is designed to meet the difficulties arising in the way of understanding divergent evolution. Advances by averages and means, while it does away with many objections urged against natural selection, offers no chance for divergent evolution, and any attempt to derive divergent evolution from

it meets the insurmountable obstacle of elimination by cross-breeding. The series of forces which tend to segregate groups of individuals by themselves, so far as concerns reproduction, offers a means of understanding divergence. Isolation, or segregation, thus becomes one of the prominent factors of evolution. We may almost reach the conclusion that each species owes its starting-point to the isolation of a group of its ancestors from free breeding with the other members of the species and thus starting two or more lines of descent. Isolation has thus acted together with the other forces to explain the origin of species. The factor suggested is acknowledged by all schools alike to be a very real one, and has done much toward clearing up our conceptions of the actual method of the origin of species.

The second additional theory is designed chiefly to meet the difficulty of determinate variation, and to show how evolution follows along definite lines, parallel to acquired variations, even if it be admitted that such variations are not inherited and that congenital variations are fortuitous. It does this simply by giving a longer time for species to wait for the favorable congenital variation, showing that meantime acquired variations will temporarily serve their purpose, being developed again and again in successive generations. It points out that many of the characters of organisms are truly acquired, and that the congenital characters themselves, perhaps, form a smaller part of the specific characters than we have believed. At all events, acquired characters

have played a very important part in the evolution of animals by directing the course of descent, even though the characters themselves may not be subject to inheritance. Acquired characters shield the individuals while they wait for the appearance, by fortuitous variation, of congenital characters of value sufficient for the action of natural selection.

There can be no question that these two theories are important contributions to the problem of organic evolution. In regard to the disputed question of whether they are a part of natural selection and, therefore, included in Darwinism we need attempt no decision. They certainly represent aspects of the problem not recognized until recently and may therefore be looked upon as actual contributions to our knowledge of evolution.

In regard to the last theory outlined in this chapter little need be said. It is purely imaginary and adds nothing to knowledge. It is interesting, since it comes from Weismann, and it may be of value as suggesting that the germ plasm may be subject to variations independent of the body holding the germ plasm. Beyond this we can hardly regard it seriously, although it must be recognized that if we could accept it as true it would solve most of the difficult problems left in the way of natural selection.

# CHAPTER VIII

## NEW LINES OF INVESTIGATION—VARIATION

IT is evident that the discussion of the method of evolution, as it has been outlined in the preceding chapters, has been almost entirely of a theoretical kind. It has been a balancing of theory against theory, suggestion against suggestion, hypothesis against hypothesis. Of course each theory is based upon observed facts. But the amount of hypothesis has become greater as the years of discussion have passed, until we have finally, in the last theory of Weismann, reached pure imagination, unverified by fact. It remains for us to consider what is being done to-day in the way of the collection of direct observations of facts bearing upon organic evolution.

As we consider these theories altogether we are confused with their claims and counter-claims. The advocates of one theory advance what seem to be unanswerable arguments, but they are met by their opponents with answers that seem equally satisfactory. Every example advanced by the Lamarckians receives an explanation by the Weismannians without the aid of the Lamarckian factor.

The advocates of the theories throw probabilities at each other and continue to discuss the subject in an almost endless round of theory and speculation. This is especially true of the discussions of the two main theories. Each has been showing up its rival in a very bad light and each explains everything to its own satisfaction. When we reduce the matter to its simplest terms the result appears to be essentially that, thus far, the question is reduced to one of a balancing of probabilities. When one side says that it is inconceivable that such a character as the peculiar angle shown in the branches of blood-vessels, a pretty constant feature in certain types, could have been developed by natural selection of congenital variations involving the destruction of individuals that do not happen to have just these angles, and then the other side says it is perfectly conceivable, since we cannot tell what exigencies may have determined the animal's struggle for existence, there is no way of deciding between them. When it is insisted, on the other hand, that many specific characters are not and cannot be useful and could not, therefore, be developed by natural selection, and, on the other hand, that we do not know enough about the animals in nature to warrant a conclusion that any character may not be of great utility, it is clear that we cannot advance in this direction any further by simple discussion.

There has naturally arisen a deal of dissatisfaction among scientists over such fruitless discussion. In recent years, especially, the younger naturalists have mostly abandoned these theoretical matters as

offering little promise of advance. They have even ceased largely to discuss evolution at all, since they take the general theory as demonstrated, but think we have as yet insufficient data to determine the method of the origin of species. They are turning more directly to nature, to see if observation may not give an answer where discussion has failed. The younger men are leaving the question of Weismannism or Lamarckism to decide itself as observations accumulate. Some go so far as to reject both theories, since they are unproved, and others regard it as futile to continue the discussion concerning them. There is a general feeling that little more can be obtained by further discussion of such purely theoretical problems, no matter how many subordinate hypotheses may be brought to their aid. If we are to advance further and learn more about the real forces producing the origin of species it will not be by any further debates over the probabilities of this or that or the other theory. Such debates represent the spirit of yesterday rather than the spirit of to-day. We meet now with a strong demand for research into nature to determine by observation, if possible, exactly *how species are being modified around us*, rather than for a continuation of the discussion of how we may imagine that they may have been produced.

It must not be supposed, however, that such a position at all depreciates the great value of the discussion which followed Darwin's promulgation of the law of natural selection, although some biologists insist that Darwin actually retarded science.

This discussion was a necessity and it was, indeed, the only advance possible at the time. Naturalists could not gain an idea of how to carry on research until after their views of nature had been moulded by such discussion. Twenty-five years ago they would have been at great loss to study evolution of species from actual observation. The discussion that has occurred was necessary, first, to place the idea of evolution upon a firm basis, and, second, to present clearly before us the actual problems which need investigation. No one will question that the study of nature has been most exceptionally stimulated by the discussions over the theoretical problems arising around natural selection. But, none the less, there is a feeling that we have proceeded along this line as far as there is any promise of results. The next advance must come by gaining more information of nature and not by developing theories.

Just how to study this problem is no easy question to answer. It has appeared that the subject may be attacked from at least two different standpoints, each of which has attracted its students. From the discussions that have preceded it has become evident that the secret of the origin of species must lie in the matter of variation, and that this, together with the problem of heredity, must be based upon the properties of the life substance. Variation and the properties of protoplasm thus offer the most promising fields, and in these two directions the modern student is largely turning his attention.

*Studies from the Standpoint of Variation*

Variations have been prominent matters for study since Darwin pointed out their importance and contributed his monumental set of observations upon the subject. From the time of the publication of Darwin's theory of natural selection the general interest in the theoretical aspects of the question, and the fascination of such studies as embryology, has led to a considerable neglect of the monotonous and rather uninteresting, although highly important, task of collecting and studying variations as they are found in nature. But the gradually growing conviction that in the problem of variation is to be found the key to the method of evolution has finally led to the renewed systematic study of variations as they occur among animals and plants in nature. To-day there are a great number of students patiently pursuing this somewhat difficult task. We are thus brought back to the further consideration of some of the topics considered in Chapter III.

The task is a difficult one, not because it is difficult to get data, but rather because of the abundance of such data. Variations are found on every hand; but the difficulty is to get anything like a method of study which shall teach conclusions that mean anything. There is little significance now in a collection of examples of variations among the individuals of a species. Such a collection might fill volumes and, indeed, be continued almost indefinitely, for variations from the specific type are more numerous than adherences to it. But the collection

would be simply useless. It is only as such variations are studied in their relation to certain laws or certain general facts that they begin to assume any meaning. A collection of facts is no longer a study of variation. The naturalist who really contributes to knowledge is the one who learns of the laws in regard to their appearance. Some of the suggestive methods of study we will briefly notice.

### *Variations around a Mean*

This subject, although one of extreme importance, need only be referred to, since it has already been considered in a previous chapter. The study of such variation is very laborious, since it involves the careful measurement and comparison of thousands of individuals. But since we have learned that, in general, we must look upon the advance of evolution as taking place by the preservation of individuals above or below the mean in respect to the development of organs, such studies of variation are of the greatest significance. They already show that among ordinary individuals departures from the mean occur to no inconsiderable extent, and are certainly sufficient to be of selective value, provided it be of advantage to the individual to increase or decrease the efficiency of any organ. For example, it is found that in the length of the wings of birds there is just that kind of departure from the mean necessary to provide for a lengthening of the wing, should it prove advantageous. Some of the birds have longer wings and others shorter ones than the

average, and hence no suggestion of determinate variation is needed to account for them. If in the struggle for existence the long wings are more useful than short ones, and if that struggle is severe, it will follow that more birds with short wings will die and thus the next generation will be descended from the survivors which have the longer wings. If, then, these variations are congenital it will follow that the next generation will have wings longer on the average than the last generation. In other words, this study of variation shows exactly the condition of things among animals and plants which would lead to natural selection upon the principle of averages and means.

It must be noticed, however, that this conclusion assumes that these variations are congenital and not acquired. But this is by no means certainly the case. Thus far no satisfactory means has been suggested for distinguishing between these two classes of variations. For this reason the conclusions from these statistical studies of variation lose much of their significance. This fact is usually not considered by those who are collating the data on variation. They commonly collect and classify the facts with the assumption that they are collecting material for the study of evolution, but without considering that possibly many of their variations are individual, not inherited, and hence have nothing to do with the problem of the origin of the innate characters of species. Recognizing how profoundly the individuals are modified by the environment, it is plain that perhaps many or most of these little differences

between individuals may be due simply to the condition of their life, and if so, they do not furnish the data for natural selection that has been assumed. Such a mere cataloguing of departures from a mean fails to show that there are any congenital variations. For all that we know, all the individuals may inherit practically similar plastic nature and these variations be due to the direct action of the environment upon the individual.

Somewhat suggestive results have been obtained by comparing the variations in large numbers of young individuals with those of the adults of the same species. The young animals are found, in some cases, to depart more widely from the mean type than the adults. This is thought to indicate that, as animals are destroyed in their battle for life, it is those that depart most widely from the normal that are eliminated, leaving finally those that depart the least, a conclusion certainly in accordance with the theoretical conception that natural selection does exterminate the extreme forms. These particular measurements, which have been made by Weldon upon crabs, have given another important result. When the measurements of different years are compared it is found that the normal type is changing rapidly. Measurements made at intervals of only two or three years show a very marked change in the normal type. The change in this particular case has been found to be due to the increase of the amount of muddiness in the water and it is particularly interesting as showing three things. First, that changes in conditions do produce a change in

the normal type of a species. Second, that the change of type in a species advances, not by the selection of a few favorable variations, but by the advance of the whole group of animals along a definite line, just as it would do upon the principle of selection of averages. Third, that species actually change with great rapidity when the conditions require it, not demanding the thousands of years which many naturalists have supposed, but actually changing under our eyes, if we will take the trouble to study them in the proper fashion. The importance of this conclusion can hardly be overestimated in view of the oft-made claim that there has not been sufficient time since life first appeared on the earth to account for the origin of the present animals and plants by evolution.

### *Relation of Variations to the Environment*

This subject is manifestly one of the greatest importance as indicating whether the forces of evolution are primarily internal, as Weismann thinks, or external as the Lamarckian assumes. There are several methods of studying the subject. First, we may study the effect produced by manifest changes in natural conditions. For example, if an animal is introduced into a new country where the conditions of its struggle for existence are changed, there is offered a valuable field for the study of variation. A comparison of examples of the English sparrow introduced into America offers opportunity for the study of the same species under different conditions.

Animals and plants upon oceanic islands are almost withdrawn from the ordinary struggle for existence and present favorable objects for study. Among plants the opportunity is much greater since the horticulturist can so easily change the conditions under which a plant grows, and the variations under the new conditions offer a most fertile field for study. Such attempts to associate variations with external conditions are evidently of much more significance than the simple study of the shapes and sizes of the parts of animals, and more likely to lead to valuable results, since they offer observations which may lead to disclosures of the causes of variations.

Although this line of work is very new, certain important conclusions are already apparent. Such studies seem to be showing that variations are dependent upon conditions. When conditions change, either those of food or climate or those associated with the struggle for existence, changes arise among organisms. It appears also that in some cases, at least among plants, these variations are transmitted by heredity and therefore become congenital. Many are, however, doubtless simply acquired by each generation as the result of similar influences affecting animals of successive generations. In general the results thus far reached tend to support the view that we must find one of the causes of variation in the changes of the environment and not simply in a chance mixture of germ plasms. The closer the connection found between the changes of the environment and the variations among organisms, the more clear is it that to the action of the environment

must be attributed in part the variations among animals.

The question of the relation of the variations to external conditions is of such fundamental importance that it has demanded consideration from various standpoints. This subject has been most prominently brought forward through the influence of American naturalists, and it has been the study of fossils in particular that has forced the matter to our attention. The great collection of fossil mammals in American museums has made possible a study of the course of evolution among larger animals, almost step by step, and it has convinced our paleontologists that external forces, perhaps the Lamarckian factors, have played the important part in this history. At all events the results are curiously interesting. They show how wonderfully the various parts of the skeleton, for it is the skeleton that has been chiefly studied, have become adapted to the action of mechanical forces. Weak joints have become strengthened by the development of interlocking bones. Smooth bones have become provided with ridges and furrows where they rubbed together so as to produce interlocking joints. Parts which have ceased to be used have grown small and then disappeared, while other organs have developed in regions where especial strains appeared. Teeth have developed tubercles and depressions in positions corresponding to wear. The backbone of the primitive vertebrate, which was originally undivided into segments, became broken into exactly such sections as would be produced by the

mechanical motion of flexing the body from side to side. And so on throughout the series. Very clearly has it been shown that the numerous changes which have been appearing in the development of animals through the recent geological ages, are just such as would have resulted from the direct effect of the actions of the animal, if we could assume that the effects of these actions could be inherited. If, for example, an animal with an undivided rod in its back should bend its body from side to side, as the early fishes did in swimming, this motion would tend to break the rod into sections, and if bony matter were now deposited in the sections, the joints between them remaining unossified to make motion possible, there would be produced vertebræ almost exactly such as are found in the early types of vertebrates. These naturalists have ingeniously shown how, in other parts the body, the influence of impacts and strains upon the skeleton would produce exactly the course of development which has been traced in successive ages in developing mammals. The evolution of the vertebrate skeleton has, beyond question, taken place along lines parallel to the acquired characters which would result from use and disuse.

It is needless to give further details, for the lesson from them all is the same as the lesson from each example. The question is not as to the existence of such facts, but as to their meaning. Those who have collected the data have generally thought that they represent a series of instances where external conditions have produced the variations

which have determined the evolution. Upon the surface they certainly seem to do so. That just such characters are produced among individuals by use and disuse is everywhere recognized. That some of them are now truly congenital, and not produced in each individual independently as acquired variations, is proved by the fact that they are developed in the embryo before there is any opportunity for the development of acquired characters by use and disuse. Whatever may have been their original cause they are now inherited characters. The whole series thus becomes intelligible upon the assumption of the inheritance of acquired characters. But to conclude that they had their origin in the effects of use and disuse is not strictly logical. The Weismannians are not blind to the facts, but explain them wholly by natural selection. They admit, of course, that such characters may indeed have been acquired by individuals, but if they have been they were not inherited. They tell us that each of these characters that became fixed as a part of the race inheritance started as a variation in the germ plasm. Such variations were of course fortuitous, but they were from the outset congenital. The congenital variations that did not happen to be adapted to the body motions would be exterminated by natural selection. Hence, only adapted types would be preserved. It has doubtless been of advantage to animals to have their skeletal parts adapted to easy motion and hence all congenital variations in this direction have been preserved. Animals with backbones that did not

inherit a tendency to break into joints could not swim and would be exterminated. We can suppose that congenital variations have constantly occurred affecting the shape of bones and, of course, those would be preserved which gave the strongest joints, the freest motion, etc. Natural selection would thus preserve the type best fitted to the conditions. This type might be quite similar to that which would result from acquired characters. Congenital variations, which would be selected, may have been similar to acquired variations, but the one did not produce the other. In other words, na ural selection would eliminate animals whose skeletons were not built upon good mechanical principles, and it is not surprising therefore that those that have survived should have parts built upon a plan which may seem to have been developed by the actions of the animals.

In short, it is not clear that the study of the development of animals through the geological ages gives any light upon the origin of variations or their relation to environment. We can trace by fossils the sequence of forms and find them parallel with results which might come from use and disuse, but that the original variations which produced this succession of forms came from such a cause does not follow. Paleontologists are studying *sequence of types* and not the *origin of variations*. The Weismannian school is free to claim that all these variations have been produced originally, not by the action of the environment upon the individual, but by unknown causes, and have simply been preserved

by natural selection. Paleontologists are studying the development of type, which affects the race, and not the subject of variations, which only affects individuals.

*Experimental Evidence*

It is manifest that one of the most promising fields of research upon the matter of variation will be experimental. It is not difficult to place organisms under modified conditions and, especially among rapidly breeding animals, continue the conditions for many generations. Such a series of observations should in time determine whether changes in conditions really affect inherited characters or not. This has for a long time been done by botanists, unconsciously as well as consciously, with the result of convincing them that such changes in conditions do produce variations in the individual which may be followed by similar variations in following generations by inheritance. Tomatoes, for example, when grown in poor soil for a few generations, become stunted and then, even if their seeds are planted in rich soil, they produce plants which retain this stunted character in spite of being now grown in rich soil. How long these characters remain cannot be stated, but they are certainly transmitted by heredity for one or two generations. Botanists in general, as elsewhere stated, are quite convinced that the environment does produce a direct effect upon the inherited traits of plants and thus becomes a direct factor in evolution.

Among animals the evidence of such direct effect

of the environment is not so clear, although great changes may be produced in the individual. In illustration may be mentioned changes in the colors of insects produced by changing conditions. Poulton, for example, has found the colors to change with the surroundings. Certainly one would have hardly expected that a change in the color of objects around a larva would affect the color of the animal. But such has been found to be the case. By surrounding certain larvæ with gilt paper Poulton succeeded in developing numbers of gilt spots on the larva. Merrifield, again, has shown that great changes in color markings may be produced in butterflies by changing the temperature at which the larvæ are allowed to develop.

Similar lines of experimentation are being carried on in many other directions. Indeed, *experimental evolution*, as it is called, has become one of the promising fields of research in recent years. The results of these experiments cannot be given here. They include the greatest variety of topics. For example, snails become small, if placed in small bodies of water, and sometimes even change from a hermaphrodite condition to that of separate sexes. Hens furnished with sulphite of lime instead of carbonate of lime make shells of this new material. Crustacea change the number of spines with changes in the saltness of the water in which they live, thus actually changing their specific characters. And so on an endless series of illustrations might be given. In general it may be said that from whatever side the subject is attacked it is found that the organism

is very easily modified by changes in the conditions, and that a great variety of types may be produced by changing the environment. Such variations are, however, commonly confined to the generation directly affected, and are probably not subject to hereditary transmission. If they were transmitted, of course there would be an end to the dispute as to the inheritance of acquired characters. At the same time some of the cases studied appear to be subject to hereditary transmission. Poulton found them, and even Weismann found it difficult to explain all the facts observed by himself except by some such supposition. It is certain that by changing the conditions we can modify many characters which are distinctive of species. By changing the saltness of the water we can make crustacea acquire characters which have hitherto been regarded as belonging to different species. From such facts we must draw one of two conclusions. Either these specific characters are inherited, in which case we have sure proof of the inheritance of acquired characters, or the specific characters in question are not inherited, but simply acquired by each individual. If the first assumption be correct then these acquired characters play a part in the origin of species. If the latter be correct, then acquired characters also play a part in the origin of species, since some of the so-called specific characters are in reality acquired by each individual and are not inborn. This brings us to an extremely important question which has arisen into prominence in recent years, as to whether specific characters are really congenital.

### *Are all Specific Characters Congenital?—Ontogenetic Species*

The discussions of the last few years have brought more and more prominently to the front the contrast between congenital and acquired characters. Botanists and zoölogists have conclusively shown that the bodies of animals and plants are subject to a very great change as the result of changes in the environment. Such changes are, indeed, not inherited, at least as a rule, but are simply redeveloped in each generation as the result of the action of the environment. Specific characters we have supposed to be inherited, but the more this matter is studied the more prominent has become the question as to whether many or most of the so-called specific characters, instead of being matters of inheritance, are not simply acquired by each individual. The fact that the organism is like its parents has previously been taken as sufficient proof that it has inherited its like characters from its parents. Specific characters, *i. e.*, characters which distinctively characterize a species, have always been regarded as inborn. But doubts are beginning to arise on this matter and naturalists are beginning to ask whether animals in their adult form are simply the unfolding of innate characters, or whether the adult is not really in considerable degree made up of acquired characters. If such should be the case it will completely change the problem of the origin of species. Perhaps the most striking and important result of the discussion of the last few years has been to bring out

this difference and to show that inborn characters are fewer than we have believed. An adult animal has certainly many characters which it shares in common with its parents; but when we come to ask which of them are inborn and which simply developed in the individual as the result of its environment, we find it impossible to answer. But the more the matter is studied the more significant do the acquired characters become.

Among higher animals, at all events, the adult characters are largely dependent upon the action of the environment. If the human infant were not allowed to use its legs they would develop into a form doubtless quite different from that characteristic of the species, a fact that tells us that the adult form is in considerable degree dependent upon use. The infant is doubtless born with certain innate characters, but to a large extent the development of these characters is dependent upon a stimulus that comes from the environment. Without use organs fail to develop, and under different environments they develop in a different manner. If the human infant, with exactly its present innate tendencies, were born in a tree and forced by circumstances to live in trees all its life, it is certain that its muscles and bones, when the adult state was reached, would be developed very differently from the muscles and bones which characterize mankind to-day. Now, if this habit of arboreal life continued from generation to generation, the new characters would constantly reappear and would of course be regarded as specific characters. Unless we knew the history they would

doubtless be looked upon as inborn, although actually redeveloped by each generation independently. We cannot fail to ask, therefore, whether it may not be that many of the characters of man, as he now exists, are acquired by each generation rather than inborn.

As soon as such a question arises the problem of species assumes a new aspect. Perhaps it may be that the actual inborn characters are few and that a great majority of features shown by the adult are acquired. Perhaps it may be that the animal simply inherits a plastic nature, and that this plastic material is moulded by the environment and will be moulded into quite different patterns as the environment changes. Color markings are important characters among butterflies, and we have supposed them to be specific and hence inborn. But if these color markings may be radically changed by changing the surroundings of the larva or changing its temperature or food, must it not be admitted that perhaps all the markings may be the result of the direct action of the environment, and not inherited? The size of a snail shell is a specific character, but it is found that this size may be greatly modified by simply keeping the animals in aquaria of different sizes. These changes in size are, of course, simply acquired and disappear when conditions change. They are not a part of the inheritance of the race. May not the same be true of the ordinary size of the shell? In other words, may it not be true that a large part of the distinctive characters of species are in reality not matters of inheritance but simply the results of

the action of the environment? Two different species of butterfly have been found to be simply temperature varieties resulting from the action of different degrees of heat on the larvæ. May not other specific characters be similarly acquired and form no part of inheritance?

It is clear that this conception puts a very different phase upon the question of the origin of species. If a considerable portion of the characters of organisms which we have hitherto called specific should prove to be acquired in each generation by the action of the environment upon the individual, the problem of the origin of species must be studied by new methods. So long as we looked upon all specific characters as inherited, so long was it necessary that our study of evolution should look for methods of modifying hereditary characters or the germ plasm, and so long was it necessary to find the origin of species in some influences which affect the hereditary process. But if we may believe that a large part, or even a considerable part, of the specific characters are not matters of inheritance at all, but simply the effect of the direct action of the environment of each individual, then the problem of species is not wholly a matter of heredity. The environment and acquired characters would then play a very important part in producing species, entirely independent of the question of their inheritance.

A character which is developed in each generation as the result of external forces acting on the individual is just as truly a specific character, provided it be constantly redeveloped, as another which is

inherited. The problem of the origin of species becomes therefore a double one. It demands, first, a separation of all characters which are truly inherited, from those which develop in the animal as the result of the environment. This is a difficult, and, indeed, an almost hopeless task. For how can we distinguish them? Any character which an animal has at any moment may be said to be in part the result of the action of the environment upon it in its previous life. Perhaps most of the characters which an animal possesses at the time of emerging from the egg might be regarded as inherited rather than acquired, although some of these may be of the nature of characters acquired by the egg rather than truly inherited. But however that may be, it is certain that the majority of characters which an animal possesses do not appear until long after the individual leaves the egg. Which of these later-appearing characters are really inherited and which are developed in the individual as acquired or ontogenetic characters? At present we can hardly see any method of answering this question. But the wonderful changes which we have learned may be produced in the characteristics of animals and plants by simply changing the environment, and thus inducing acquired characters, show plainly that we cannot explain the origin of species until we know to what extent their characters are really inherited and to what extent simply acquired. At the present time our information on this subject is very meagre. The discussion of evolution in past years has not even recognized the question. None of the laborious

studies of the statistics of variation have as yet separated these two types of variation, and all data thus far collected giving variations among individuals place in one list all variable characters, including both congenital and acquired.

After having thus separated the two classes of variations, we may be in position to ask more intelligently a second question as to how the true congenital characters came to be fixed in the hereditary process. But until we know more of the actual results of the environment in producing the host of characters which we commonly regard as specific, it is evident that we cannot hope successfully to answer the question as to the forces which have brought about the origin of species.

This conception is at the present time dividing modern biologists into two schools. The one school, which naturally includes the Weismannians, places great stress upon the germ plasm and inherited traits. The other looks upon the inherited features simply as plastic clay which is subsequently moulded by the environment into the adult. The inherited substance represents the clay bank, the environment represents the potter. The characteristics of the fully formed vase are more dependent upon the potter than the clay bank. The adult differs from the newly born individual largely in characters that are acquired and not wholly in those that are inborn, and, indeed, some would even go so far as to say that the differences between the adult and the egg are acquired purely as the result of the action of the environment upon the egg.

The debate over this problem is one of the live subjects of discussion and experiment to-day. The idea may be easily carried to extreme, for inheritance certainly counts for a great deal. In breeding pigeons a female of one species may be crossed with another species. The eggs are incubated and the young reared under identical conditions with those which would surround her young if their father were one of her own species. But the offspring all through life show the characteristics of the male parent more or less well expressed. Here evidently it is inheritance and not acquired characters that are concerned.

Without, however, exaggerating this notion of the acquired characters of species, it is certain that in the past we have too readily assumed that characters which appear in successive generations are transmitted by heredity, and we have given too little attention to the possibility of their being acquired independently by each generation. Acquired characters form an important part of the characters of the adults and this without any claim that they are inherited. Weismann, by his theory of heredity, has been of great value to biologists in forcing us to distinguish sharply between acquired and congenital variations and to recognize that they stand differently related to the matter of heredity. One of the tasks for future study must be to isolate clearly these two factors, each with its different origin, but each contributing to the origin of species. Our naturalists, perhaps, do not even yet fully appreciate the matter and are still collecting variations *en masse*,

without trying to determine what are congenital and what acquired.

It would appear, then, that we must recognize three independent realms of variation. The first is in the variability of the hereditary substance, or germ plasm, if we wish so to name it. Variations appearing here, of course, affect the offspring for many generations, so long in fact as the germ plasm retains this new character. It is upon this type of variation that Weissmannism is based, evolution being simply produced by selection of varieties of germ plasm. Secondly, we find that just as soon as the individual starts its existence, which is at the fertilization of the egg, it begins to undergo modifications produced in it by the conditions acting upon it. The different parts, cells, and organs, are placed in new relations to each other and to the food supply, and a series of changes begins which results finally in an adult. That adult must be looked upon as an engrafting of numerous acquired characters upon the original innate characters. Lamarckism claims that these second variations are engrafted upon the germ plasm as well as into the body and thus modify the inherited traits of the next generation. Third, we have the gradual modification of species, requiring many generations, which has evidently been produced by a combination of the action of the first two classes of variations, aided by elimination by natural selection. If we explain the third type of variation by the first without the second, we have Weismannism; if by the second chiefly, we have Lamarckism; if by

both first and second, we have the original Darwinism. Natural selection refers to the last of these three factors; the struggle of parts of Roux to the second, and the germinal selection of Weismann to the first. The actual method of evolution consists doubtless in the production of the third class of variations by the combination of the other two.

### *Discontinuous Variation*

By this term is meant something quite different from the fluctuations that occur on either side of a mean. They are rather the larger variations which appear suddenly and may alter the whole character of an organ, or even the whole animal. Here again the amount of data is overwhelmingly abundant and the problem is rather as to its meaning than its existence. Even in regard to such variations, striking as these sometimes are, very little is accomplished by a simple collection and description. Only as they are studied in the line of certain principles can they assume any significance. While some naturalists are to-day studying the lesser variations by the statistical method as outlined above, others are occupied in the study of these discontinuous variations. Since this topic has been considered in an earlier chapter only one or two additional points need here be mentioned.

Great, sudden variations have long been known, and the collection of more examples is not calculated to add to their meaning. The real problem, so far as relates to the question in hand, is what part such

variations play in the process of evolution. Can any real line of distinction be drawn between such freaks, which we call "monstrosities," and the lesser variations which we look upon as normal? Is there any difference in kind between what we call "sports," such as extra fingers and toes, red azaleas on plants commonly producing white flowers, etc., and the normal variations on either side of a mean? More important is the question whether such sports play a part in the origin of species, or whether they are simply departures from the normal which count for nothing in the process of evolution. Can such monstrosities be comprehended under laws so that we can understand them? Are they wholly congenital or are they due to the abnormal action of environment?

It is perhaps too early as yet to determine the final answer to these questions, but some results have already appeared of significance to our discussion. Beyond much question, as we have seen, such discontinuous variations, or sports or monstrosities, if we choose so to call them, do occasionally play a part in the origin of new types. Most naturalists, however, look upon them as relatively unimportant compared with the more abundant but smaller variations. Secondly, it is clear that they are not purely hap-hazard, but are controlled by some general laws. Certain kinds of variations are likely to occur while others are not found. If, for example, an animal has several organs in a series, like the five fingers, it is quite common to find a variation of an extra organ in the series, but, to find

a similar organ occurring elsewhere in the body and out of the series, is unknown. This simply shows that these variations are controlled by the internal forces which regulate growth, but it does n't indicate much more. These large variations are commonly such as the appearance of extra organs in a series, or their disappearance, or great change in the shape of organs. The appearance of totally new organs does not occur, so far as observation has thus far gone. It is doubtful whether, for this reason, discontinuous variation gives much aid in solving the problem of the first appearance of organs. Lastly we may notice that discontinuous variations appear to be congenital rather than acquired, due rather to variations in the germ plasm than in the individual.

### *Determinate Variation*

Perhaps no subject connected with variation is more significant than the question whether they occur hap-hazard or in definite directions. It has been the idea of Darwin and Wallace that they are hap-hazard, having, at all events, no connection with the purpose to which they are subsequently directed. They become of use through selection and not by being originally adaptive. But, as we have seen, there have been many serious objections raised to this view. The inherent improbabality of a chance variation appearing when and where it is needed has led to the claim that we must explain the *origin* of the fittest before we can talk about the *survival* of the fittest. Against this claim it has been urged that it

rests upon a misunderstanding of natural selection. When insisting that natural selection is the real cause of the origin of organs it is assumed that the variations which are selected are fortuitous, simply variations above and below the average, just such as the theory of probabilities would lead us to expect, and if so the demand for the origin of the fittest has no meaning. If miscellaneous changes in conditions or in germ-plasm mixtures produce indefinite variation in inherited characters, and if the natural selection preserves only those among them which are of use, then natural selection is a real cause of development, since it determines the survivors and thus really directs the evolution. But if, on the other hand, it should appear that variations are not simply haphazard, but occur in definite directions, if it should appear that they have a tendency to occur in large numbers of individuals at once, or that they should reoccur in successive generations, if they should appear in certain directions and not in others, or if it should be evident that the variations which produce new species are sudden, and of the character which we have called discontinuous, then the question as to why variations are of this character is antecedent to the question of their survival. Then it would appear that the real primary force which produced evolution was not survival but the force which produced these determinate variations.

If shots are fired from a machine gun in the vicinity of a metal shield with a hole in the centre, the hole will determine which of the shots will pass through the shield, and there is no need for a person

behind the shield to determine the conditions of firing the gun to explain why the shots come through the hole. Brooks, in his discussion of natural selection, has used this illustration. But he should have carried it further. If it were found that the shots from the machine gun all came in the vicinity of the target instead of flying off all around the compass in every direction, then it would be necessary to conclude that there was some directive force at work *at the gun.* In the same way, if variations are in every direction and natural selection simply determines which shall survive, then we need not ask for any directive force controlling variation. But if it be found that the variations are all in the same definite direction, then we must ask for some directive force regulating the origin of variations. The question whether there is any force in the demand for the "origin of the fittest" will depend upon whether we find variations to be fortuitous or determinate. It is not diversity, but *determinate diversity* that is difficult to explain. If it appears that variations are definite and adaptive prior to their selection, then we have something that Weismannism cannot account for.

It must be noticed that, in regard to such characters as may be supposed to develop by the selection of variations above and below the mean, this demand for an explanation of variations has little force. Upon the law of probability, about half of the animals would be above and half below the average. If it should be of value to have the organ increased in efficiency there will be plenty of individuals

existing at all times showing variations in the right direction, and it needs no theory of determinate variation to explain why there should be appropriate variations where needed. The same series of variations will continue in the next generation in an even more marked degree, provided they are congenital characters, since the survivors will have been selected from the animals with the character best developed. Thus generation after generation similar variations along similar lines will occur without any necessity of assuming determinate variation. This will of course apply in all cases where evolution consists simply in the increase or decrease in the size or efficiency of parts. But it could not explain divergent evolution nor the beginnings of organs.

Now it has been a growing conviction of the last ten years that variations are not simply hap-hazard but are determinate. This has been recognized by many naturalists working in different lines. It has been variously called, "conscious force," "self-development," "directive tendency," "determinate variation," but in all cases it is essentially the recognition of some force at work *prior* to selection, which controls variations in some way. It has appeared from the study of fossils in marked degree. When the geological succession of animals is studied it is found that the development of types progresses steadily onward in a given line. Our paleontologists have become greatly impressed with this fact and emphasize it again and again. There is no evidence of trials in various directions, such as would be expected from the natural selection of hap-hazard

variations. On the contrary there is ever a constant progress apparently toward a definite goal. After a group of animals starts on a certain line of development, it follows it with unmistakable directness. What is more significant is the fact that many kindred groups follow the same line. Where the development of the teeth is followed through long ages, it is found that in all types of mammals there is the same tendency toward the appearance of definite tubercles at certain points in the teeth, and this in such widely separated groups that it can hardly be doubted that there is some directive tendency beside the selection of hap-hazard variations.

We may find evidence of the same principle among living organisms. For example, the cyclamen under cultivation shows a general tendency toward the appearance of a peculiar crest on the petals. This crest appears in many independent plants, thus showing some general tendency toward its development, and it is actually found to increase in size with successive generations. Whenever two crested plants are crossed the progeny is likely to have a crest larger than either parent. All of this plainly points to a tendency to vary in definite lines. In man it has been shown that the little toe is undergoing a constant, although slow reduction in size. This reduction occurs in races that go bare-footed as well as among those that wear shoes, and thus seems to point to some innate tendency.

Now, although each of these classes of examples may be explained in some other way, taken altogether they constitute evidence for determinate

variation that is very strong. Indeed it is so strong that even Weismann, as we have already noticed, has felt it necessary to find an explanation of determinate variation which shall be consistent with his theories of germ plasm. It is true that there are some naturalists who insist that we have no sufficient demonstration that variations are anything more than hap-hazard, but, in general, determinate variation is recognized as one of the factors in nature to be reckoned with. If variations were simply hap-hazard, the number of individuals that did not agree with the preserved type would, on the principle of probability, outnumber the variations in the right direction many thousands to one. These must all have been exterminated and it would seem that traces of them should be found. But paleontologists do not find them. Evidence seems to indicate that evolution has been a constant advance along rather definite lines, and not miscellaneous trials of numerous variations. It has, indeed, been the belief in determinate variation that has led Weismann to his theory of germinal selection, Baldwin and others to the theory of organic selection, and many others to feel the necessity of some other factor besides simple natural selection.

### *Attempts to Explain Determinate Variation*

The study of variations which has been renewed with vigor in recent years has certainly helped us toward a real solution of the origin of species, but has not yet given us very firm ground to stand upon.

We have learned that variations are abundant, that they appear simultaneously in many individuals, that they tend to reappear along similar directions in successive generations, that they are commonly rather small, being chiefly in the size of organs, that they are sometimes of a greater extent, involving an entire change in the shape of an organ or the appearance of a new organ in a series. We have learned that they are beyond much doubt associated with changes in the environment. We have not yet obtained much, if any, information which explains the beginning of absolutely new organs, nor have we much information as to the real causes of variations. To what extent the mixture of germ plasm in sexual reproduction can be held responsible for the general facts; to what extent the direct effect of the environment may act upon germ plasm, and to what extent the effect of the environment may be responsible for congenital variations, these are questions still unanswered. The belief in the inheritance of acquired variations has certainly been losing ground in the last ten years, and most naturalists look upon this agency as a doubtful one and one of comparatively little importance if accepted at all. With all this, it is fully recognized that the origin of variations and their preservation and transmission is the key to the solution of the evolution problem.

The feeling that something is needed to explain the appearance of variations along definite lines, when and where needed, has led to various attempts to meet the demand. Weismann's germinal selection and the theory of organic selection are along

this line. But the most common way of meeting the difficulty is by supposing the existence of some inherent tendency. This idea appeared with Lamarck, who thought that all animals had a tendency to advance in structure. Later Naegeli expressed a belief in an innate tendency to progress as a force among organisms. Again Mivart found some internal force stimulating the origin of "extraordinary births" which became new species at once. The idea appears verbally in Darwin's "inherent tendency to vary." With Darwin, however, this expression simply meant that changing conditions produce variations among organisms, and this is of course not akin to the other ideas of inherent forces. Later still we find the idea in the theory of "self-adaptation" of Henslow. This "self-adaptation," in spite of all that is said of it by its author, is hardly more than the idea of some unknown force pushing organisms onward. It is also found in the writings of other authors who speak of "growth force" or "bathmism." Under these terms the authors do not always mean the same thing, but in general such expressions appeal to the idea of the organism being influenced by some force which is constantly trying to find expression, a force that is trying to push organisms onward into vigorous activity. It is this force, for example, that is stimulating the production of buds and branches, a force ordinarily kept within bounds but ever pushing its way to the front to stimulate the formation of new organs. This force is supposed to be most vigorous in the young condition and disappears with old age,

but is renewed with sexual reproduction. Now one can hardly pretend to doubt the existence of something corresponding to what has been called "growth force." But to give this force a name does not help toward the solution of the organism. We see that the young grows faster than the adult, that plants are ever putting forth new buds, that variations occur in definite lines, that animals progress constantly. We may perhaps express these facts by speaking of growth force. But after having done so we are no whit nearer an understanding of the matter. By means of a name we have tried to imagine we have explained certain phenomena. It may represent a fact, but it explains nothing.

In regard to all these suggestions one general criticism may be made. They are all purely verbal and explain nothing. To say that animals have an inherent tendency toward progression is saying nothing more than that they do progress. To say that extraordinary births sometimes appear is exactly the same thing as saying that there is an inherent tendency to produce such births. To say that animals are actuated by growth force is saying nothing more than that they grow vigorously. To say that variations are determined by some inherent law is only saying that they do not appear to be haphazard. In all cases we fail to place ourselves any nearer an understanding of the organism by giving a name to forces, or forming a theory of evolution based upon them. The problem is to explain the facts and not to include them under a new name. No one supposes that these various forces,—growth

force, inherent tendencies, etc.,—are distinct forces in the sense that electricity is a force. If anything is meant by the terms it is simply that the actions of the protoplasm are such as to produce results of the character found. The problem which we are trying to solve, is *why* it is that protoplasm acts in these ways and what the real forces are which have given rise to the existing order of things. If one tells us that there is an inherent-tendency upward, we must simply ask what produces that tendency and why it should be upward rather than downward. This is the very question that the evolutionist has been trying to solve and we are no better off after we have invented a few names for imagined forces.

It would hardly seem necessary to mention such a simple fundamental principle were it not that this sort of jugglery is ever cropping out anew. Doubtless the authors of these terms see clearly enough that they are only furnishing a name for a series of facts, without an explanation. They are perhaps formulating a little more clearly the lines of activity of orgainsms, but they are not giving any intelligible notion of the method of descent. Not all of their readers are equally logical and many could be found who see in the inherent tendency to progression an actual force explaining evolution. It is necessary here, therefore, to insist that such attempts to account for evolution of organisms are not explanations at all, but simply statements of the facts in different words. If we are ever to comprehend the method of the origin of species we must find

our information in some other way than simply by giving a name to some force which we dimly feel the necessity of supposing to exist. All theories of inherent forces must then be regarded as irrelevant to the main problem at issue.

### *Summary*

The theoretical discussions of the method of evolution have thus far led to no satisfactory conclusion, and the younger naturalists have become convinced that any further advance must come from the study of nature itself rather than from any more discussion of theory. The two topics which apparently hold the secret of the problem are variation and the properties of protoplasm. Naturalists are to-day eagerly attacking these two subjects.

In the study of variation the difficulty has been to determine a method of collating the facts, which is likely to teach anything, for mere collection of data has no longer any significance. The careful measurement of parts and noting their relation round a mean has offered some valuable suggestions, since it has shown that variations occur in nature of exactly the character needed to explain the evolution of type by averages and means, provided we can assume that these variations represent congenital traits. This is as yet, however, merely an assumption and not demonstrated. This study of variation is showing to us the actual operation of natural selection and possibly the rapid formation of new species under our eyes.

The relation of variation to the environment is studied in two very different ways. One is by studying the effect upon organisms of placing them in new conditions. The result of this study has been to show conclusively that variations are in considerable degree caused by changes in the environment, such external changes being followed by variations in the structure of animals and plants. In asking whether such effects are inherited we find little proof that they are, but are forced to the conclusion that a considerable part of the so-called specific characters of organisms are not inborn characters but simply acquired by each individual, independently, in successive generations. This gives a new conception of species which very decidedly alters the problem of the method of the origin of species. With the idea that specific characters are in considerable degree acquired, the problem of the origin of species is one which demands the consideration of both acquired and congenital characters. The second method of study has been through fossils, and consists largely in showing how accurately the development of the vertebrate skeleton has been parallel to the results which would be expected, in accordance with the assumption of the inheritance of the effects of use and disuse. But these facts, striking as they are, can also be explained by natural selection without such inheritance, and are hence inconclusive.

The study of variations which are of greater extent than the slight departures from a mean appears to be showing that discontinuous variations do play

a part in the origin of species. Lastly, we have seen that a general view of variations is slowly, but apparently surely, convincing students that they must be looked upon as determinate. If such a conception is held, then the problem of the origin of species becomes a problem of determining the causes of these variations. In trying to find such a cause different scientists have taken a refuge in various verbal explanations, such as " inherent tendencies", etc., which really explain nothing and do not aid at all in the solution of the problem of the origin of species. In general, then, the study of variation has as yet given no very certain ground upon which can be based a theory of variation, nor have they told very clearly to what forces these variations are to be attributed. Beyond question they must be traced to the properties of protoplasm.

# CHAPTER IX

## STUDIES OF PROTOPLASM

FROM whatever side we look at the subject we are forced to the conclusion that evolution has been the result of the activities of the living substance. Whichever of the contending theories be correct, the process of descent is founded upon the properties of protoplasm. If we adopt Lamarckism, we must refer the powers of the body to develop acquired characters to the properties of protoplasm. If we adopt Weismannism, then the appearance of congenital variations is traced to the properties of that particular kind of protoplasm called germ plasm. Evolution is based upon variations, and variation is a property of protoplasm. Heredity is an equally important factor, and this again is a property of protoplasm. Although selection and isolation and other external forces direct evolution, after all, the foundation of the process must lie in the properties of the life substance, or protoplasm, as it is still commonly called. To the composition of this substance, must be traced the property of living

things to vary, and to vary in definite lines. It is not surprising, therefore, to find naturalists giving to-day more and more attention to the properties of this substance, with the conviction that here is the most promising field for future discovery of the laws that have been involved in the building of the animal kingdom. There remains for us now a review of what is being done in this direction.

### *Protoplasm not a Chemical Compound but a Mechanism*

From the early years of the discussion of evolution it has been a favorite belief that protoplasmic problems are chemical problems. Under the stimulus of Huxley's creation of *Protoplasm; or the Physical Basis of Life*, there has been a general tendency to look to the chemist for the solution of the properties of this substance. The chemist found himself capable of making, by chemical means, many compounds which had hitherto been regarded as produced only through the agency of life. By purely chemical combinations he began to climb the ladder which led from the simple elements to the most complicated. At the bottom of the ladder were the elements. The lower rounds were such bodies as $CO_2$, $NH_3$, etc., while higher up were such substances as starches and fats. Still higher were albumens, while at the very top protoplasm had been supposed to stand. Now, since the chemist found himself rapidly climbing this ladder, it was natural for him to assume that he would some day

reach the top and make protoplasm. Predictions to this effect have been freely made.

With such views in mind biologists began to speak of "chemical evolution" as a phase of evolution preceding the evolution of life. They began to speak of the probability that in the early ages of the world's history conditions were such as to make it possible for the chemical elements to unite in different combinations from those that normally occur to-day, and to tell us that the compounds thus arising became more and more complicated until finally protoplasm made its appearance. The origin of life was thus one of chemical evolution due to chemical forces. For a quarter of a century following Huxley's famous address the solution of the properties and the origin of protoplasm were sought confidently among chemical forces.

The aspect of the question has to-day greatly changed, and such a simple view of the origin of protoplasm is no longer tenable. For fifteen years or more the modern microscope has been disclosing facts regarding this life substance which have demanded completely new views, and these facts have become of significance enough to be grouped together under a new branch of biological study called *Cytology*. The disclosures of this new branch of study are surprising and unexpected. So far as we know, *unorganized protoplasm does not exist*. The properties of life appear to be manifested by nothing simpler than the organic cell. Everything that grows and reproduces is in some degree differentiated into cells, and the cell seems to be thus the simplest

condition of matter which can manifest the properties of life. But the cell is anything but simple. It consists of many parts acting in adjustment to each other. The more it is studied the more complex it appears. Some idea of its complexity may be inferred from Fig. 11, which shows a cell plainly made of many parts. The intricacy of the structure is further emphasized when we study its activities. Reference to Figs. 14–24 gives some idea of the actions of a cell. As the cell is studied alive these separate parts are found to carry on various actions and the whole cell shows an intricate interaction of parts. With its fibers and threads, its centrosome and microsomes, which seem to be pushing and pulling, acting and reacting upon each other, the cell behaves very differently from any chemical compound. It acts rather as a machine. It must be regarded as a mechanism and cannot be called a chemical compound. Its properties are the properties of the cell as a mechanism and not of the cell as a chemical compound. Doubtless these properties may, at the end, be traced to chemical forces, just as the activities of the steam engine may be traced to chemical forces. But chemical forces do not explain the motion of the steam engine. Its motion is explained by its mechanism. So with the cell. While chemical forces doubtless lie at the foundation of living activity, the actions of the living cell are to be explained by its *mechanism* rather than by its chemical nature. If we trace variation to "organic composition" it must be to the mechanical rather than the chemical composition of this substance.

With this conclusion the conception of protoplasm as a chemical compound disappears and the notions of chemical evolution must be radically changed. It is true that the cell figured in Fig, 11 is by no means the simplest cell. It is rather one of the most complex. The simplest forms of life certainly show less complicated machinery than this cell. But the principle remains the same wherever we look. Even the simplest forms of living matter are not chemical compounds. The simplest form of living matter that we know is found in bacteria; but we are fast learning that even these minute bodies have a structure within, and are in no sense simple chemical compounds. They, too, are mechanisms, simpler indeed than those of higher cells, but none the less mechanisms. Whether there be still simpler organisms we do not know. Certain it is that these organisms, which appear to be the simplest bodies that exhibit the properties of life, are not chemical compounds but mechanisms.

Now the significance of these facts is great. So long as we could look upon protoplasm as a chemical compound, the problem of its origin was a chemical one; but the moment it appears to be a mechanism we see that chemical forces are entirely inadequate to explain it. Chemical forces do not make machines. In the previous chapters of this work we have been considering the attempts which science is making to explain the origin of adaptive mechanisms. If protoplasm were a chemical compound no such necessity would here exist, since chemical forces are sufficient to explain chemical

compounds. But, finding that protoplasm is a mechanism, we see that to explain its existence we have exactly the same sort of problem that we have in explaining the adaptive organs of animals. Between the simplest forms of life which we know and the higher forms there is a long series of structures, built up by forces we have been considering in previous chapters. We are now becoming aware that between this simplest form of life and the most complex chemical compound there also exists a long series of intermediate steps, built up by forces which we have not yet fathomed, but which must be in some sense mechanical forces and cannot at all events be chemical. In dealing with the problem of the evolution of protoplasm we have not a question of chemical evolution. We can no more hope to explain the evolution of the living cell by chemistry, than we can explain the production of a steam engine by chemical forces.

It will easily be seen, then, that the study of the cell and its activities is offering a new set of problems for solution. When it is remembered that all of the fundamental problems of evolution have been reduced to the actions of life substance, that variation, reproduction, and heredity have all been traced to the properties of life substance; when we remember the complexity of the simplest living unit, the cell, it becomes clear that it will be by the study of the structure and properties of protoplasm that investigation must be pushed if we wish to learn more of nature's method of producing species. The problems of evolution must be studied along lines of Cytology.

### *Chemistry and Mechanics of Protoplasm*

Upon these topics comparatively little has yet been learned which appears of much significance to the general purpose of explaining life and variation. Chemistry has disclosed within the cell machine a large number of chemical compounds. It has shown them to be remarkable chemical bodies, and has lately hinted that they possess chemical properties of even unique nature. But chemistry has yet given us no information which aids toward the solution of the activities of protoplasm.

The problem of the mechanics of protoplasm is hardly more advanced. Whether protoplasm consists of a mass of foam or of a network of fibres holding liquids in its meshes is still somewhat of a disputed matter. The more the living cell is studied, the more intricate appears to be its structure, but what that structure is we do not yet know. Our knowledge of this mechanism is entirely too inadequate to enable us to explain its activities. We can see that the substance has powers of action but we have no understanding of the activities.

An important part of the evolution problem is, of course, the origin of life, which appears to mean the origin of the first protoplasm. Upon this subject it must be confessed we are in as deep ignorance as ever. Indeed, if anything, the disclosures of the modern microscope have placed the solution of this problem even further from our grasp. So long as we could regard protoplasm as a chemical compound, definite though complex, so long was it

possible to believe that its origin in the past geological ages was a simple matter of chemical affinity. It was easy to assume that under the conditions of earlier ages, when chemical elements were necessarily placed in different relations to each other from those of to-day, chemical combinations could arise which would result in the formation of the complex body, protoplasm. This has been the supposition that has laid the foundation of various suggestions as to the origin of life. But, having now learned that this life substance is not a chemical compound but a mechanism, and that its properties are dependent upon its mechanism, such a conception of the origin of life is no longer tenable. In its place must be substituted some forces which can build a mechanism. But even our most extreme evolutionists have not yet suggested any method of bridging over this chasm, and at the present time we must recognize that the problem of the origin of life is in greater obscurity than ever. The origin of chemical compounds we may explain, but their combination into the organized machine which we call protoplasm is, at present, unintelligible.

### *Developmental Mechanics*

Within the last few years there has arisen a new method of studying some of these general problems. We have seen that one of the most prominent questions to-day is, whether evolution has been due to the selection of variations which appear in the germ plasm or whether variations which appear in the

body also play a part. Now the study of protoplasm is offering a method of distinguishing between these two classes of characters, and thus perhaps in the end of showing how far each has played a part in the origin of species. There has recently arisen a new branch of experimental study called *Developmental Mechanics* (*Entwicklungsgeschichte*), which endeavors to distinguish between inherited and acquired characters by experimenting upon the developing egg.

In the fertilized egg must be contained the physical basis of heredity (germ plasm), and in the development of the egg we must have the unfolding of this substance. If we can follow the unfolding of this germ plasm we may, perhaps, unravel some of the problems of heredity and separate congenital from acquired characters. For nearly half a century our naturalists have been studying this unfolding in the study of *Embryology*, and by means of it have been trying to learn of the laws of life. But in the past the embryologist has been guided chiefly by the very suggestive conception that the embryology of an animal repeats its past history and will, therefore, furnish a key to the past evolution of the animal kingdom. The study of Embryology has, in the past, been chiefly a study of *phylogeny*, *i. e.*, a study of past history. Under the stimulus of this idea, investigations have been pushed in all directions and a vast amount of information as to the evolution of animals has been obtained. But embryology has not answered all the questions set for it, and there is a tendency at the present

time to decry this study as delusive. It is beyond question that the results have been somewhat disappointing. It was at one time hoped that it would disclose with considerable accuracy the history of animals, and so completely teach us that history as to give a very thorough knowledge of the laws of evolution. But in both respects it has failed to meet expectations. As a source of history it has been found to be subject to so many misleading irregularities that, in large numbers of cases, the significance of the numerous conflicting facts cannot be determined. Beyond doubt, the study has been of great value, and modern zoölogy is greatly indebted to the discoveries of embryology. But on the whole the results have been disappointing. There is a growing feeling that all the important teachings of this subject have already been learned, and future study is likely to multiply details without teaching much more. Moreover, it has been felt that this study has not yielded so much in regard to the general laws of evolution as was hoped. In the animal kingdom it has told us many facts as to the general plan of evolution. In the vegetable kingdom it has told us very little of this nature. In both kingdoms its teachings are so confused by modifying conditions that it is difficult to draw any definite conclusions. In short, while the study of embryology has been of great value to zoölogical science, it has, so far as general teachings are concerned, failed to come up to expectations, and at present it offers little promise of more valuable results. We find, therefore, that the naturalist of

to-day who is interested in solving the problems connected with the evolution of animals is turning his attention in different directions. Embryology does not attract students to-day.

But a new phase of the same general subject is beginning to assume a great prominence as a means of studying the laws of heredity and protoplasm. It is plain that the germ plasm and its unfolding must involve the most important secrets of evolution and life. But how are these secrets to be disclosed? Manifestly, the most natural method would be by putting the egg under unusual conditions. The egg develops normally in a definite environment, and the adult animal is a combination of the characters of the germ plasm plus the acquired characters impressed upon the developing egg by the environment. If we can separate the two we shall advance far toward determining the part each type of variation plays in the evolution process. Now, if we can put the egg into entirely new conditions, we may determine how far acquired characters produced by the new environment may modify the animal and thus obtain data for separating acquired (ontogenetic) from congenital traits. To accomplish this, the egg is now being subjected to a most exhaustive study from the moment that it can be first distinguished as an egg, through all its stages of growth as an egg, through its fertilization and its early development. It is placed in a variety of unusual conditions. It is cut to pieces and the history of the fragments studied, and every possible environment substituted for the normal.

According to the idea that all specific characters are inborn, which is the usual view, and that evolution has been produced simply by the selection of congenital characters, the germ substance in the egg must contain a structure practically as complex as the adult. Weismann, as we have seen, thus looks upon the germ plasm as extraordinarily complex, and he has drawn an imaginary picture of that substance. This conception finds every feature of the adult represented in some way in this complex germ plasm. Such a view looks upon development of the egg simply as an unfolding of something already present in it.

In the last century certain naturalists held the position that in the egg there was present a miniature animal exactly like the adult except in size, and that the development of the egg was simply the growth of this little individual. The development of the egg was thus simply the growth or "*evolution*" of an individual contained in the egg at the beginning. This conception of development was called "*evolution*," a term which thus at that time meant something entirely different from the word as commonly used to-day. An evolutionist of the last century was simply a naturalist who thought that each egg contained a miniature adult, and that development was thus simply its unfolding. It will be seen that the position of Weismann is simply a modified form of the same theory. To be sure, Weismann does not think that the egg contains a miniature adult, but he does believe it to contain a germ plasm which has a structure of great

complexity corresponding to that of the adult. He still looks upon development as the unfolding of this germ plasm, or the making manifest of characters which were simply potential in the germ plasm. It will be seen that this conception of the egg is a part of the theory that bases the method of evolution entirely upon the selection of congenital variations.

On the other hand, the "evolutionists" of the last century were opposed by the "*epigenesists*," who denied that the egg contained a miniature adult, but claimed that the egg was simple and the adult was gradually built out of it as a house is built out of bricks. This school of scientists has demonstrated its position against the earlier "evolutionists," for it is easy to prove that the egg does *not* contain a miniature adult, and that the embryo is gradually built up during development. But the new form of the old "evolution" theory, which Weismann holds to-day, is not so easily disproved. The "epigenesists" of earlier days are represented to-day by a school of modern students of developmental mechanics that emphatically deny Weismann's conclusions as to the great complexity of the germ plasm. They insist that the adult characters are in a very large degree due to the action of external forces upon the very unstable egg protoplasm. The egg is comparatively simple and the complexity arises during development. As the egg develops, the parts are being constantly placed in new relations to each other, and these new relations ever produce new effects. Complexity thus arises during the development of an originally compara-

tively simple egg. Development is not an *unfolding* but an *acquirement* of complexity. Of course, the supporters of this school admit that there are differences in the eggs at the start. Otherwise they could never explain the appearance of a hen and a duck from two eggs under the same hen But they insist that the differences are comparatively slight and that there is no such complexity as Weismann supposes, this complexity slowly arising as the result of the action of new relations. The differences between the eggs are not commensurate with those of the adults, but only sufficient to start the eggs into different lines of development. The adult characters arise during the development as the result of external forces. This view is evidently a part of the conception of *ontogenetic species* already discussed on page 351. It is clear enough that if " evolution " is the outcome of Weismann's view of the origin of species by variations in the germ plasm alone, this new phase of " epigenesis " is a logical outcome of the view which looks upon acquired or ontogenetic characters as playing an important part in evolution. If the adult is completely represented in the egg, then we must look upon species as having been produced by congenital variations which affect this germ plasm. The origin of a new species would then be simply the building up of a new kind of germ plasm. If, however, the adult is not wholly represented in the egg, but its characters are in considerable degree produced by the action of external conditions upon the unstable protoplasm, then clearly the environment has

decided effect upon the origin of species. With this idea it will follow that the class of characters which we have called acquired form a very large part of the characters of animals and plants, and our problem in explaining the method of the origin of species will be, not only to account for the building up of the germ plasm, but also to determine the relation of the variable protoplasm to its conditions. The one view must find congenital variation the sole basis of descent, while the other will find acquired characters playing an important part, independent of the matter of inheritance. It is evident that our final conclusion as to nature's method of building species will depend upon the conclusion reached as to the nature of the egg plasm and the laws regulating its development.

Up to the present time the new study of developmental mechanics has been devoted largely toward deciding between these two views of the nature of the egg plasm. It cannot be stated that any very positive result has yet been reached. But if one is to understand the present aspects of biological study, it is necessary to know what sort of work is being carried on in this line of research, even though the conclusions are very scanty. A brief outline of the sort of experimenting which is being carried on will therefore be in place here as a conclusion of our review of the method of evolution.

### *Experiments in Developmental Mechanics*

We may notice first a simple question, apparently capable of easy solution. It is admitted by all that

there must be in the egg some substance which is the basis of heredity, and which we may call germ plasm. Now the first step in the development of an egg consists in the division of the egg into two parts, and the question arises at once as to how this germ substance is divided. Does it begin to differentiate in such a way that each of the two first divisions receives a different kind of material, or does it divide in such a way that each division receives identical halves? If Weismann's view of the egg be correct, manifestly each of the resulting two divisions should be capable of producing only half of a complete animal, since the germ plasm is materially divided, while if the "epigenesists" are right, then each cell should be identical and capable of producing a whole individual under the right conditions. According to Weismann's conception, the division should result in a differentiation and each half should thus have only half the powers of the original egg. According to the opposing view, each should be simply smaller, but should contain undifferentiated protoplasm capable of producing a whole animal if placed in proper conditions, since it is the conditons rather than the inheritance that produces the adult. To settle such a question as this, experiments have been devised of isolating one of the first two parts of a dividing egg by itself and seeing what becomes of it. This is sometimes done by killing one of the first two cells with a hot needle and watching the other, sometimes, by shaking the eggs until the cells separate, and sometimes, by actually cutting them apart with delicate

instruments. Again, after the egg has divided into four parts, and then into eight, the same questions arise and the same methods of experiment suggest themselves.

Already such experiments have become quite numerous. They have been performed upon different animals and by many different observers. The results have been in the widest conflict. Sometimes each half-egg develops a half-embryo, having only one side or one end, and thus seeming to indicate that there is a differentiation of germinal material such that each cell of the divided egg receives the germ substance which is to control the development of one half of the animal, just as Weismann would suppose. But on the other hand, in other animals the reverse occurs, and each half egg develops into an animal differing only in size from the normal animal developed from the whole egg. Here it would seem that Weismann's idea of differentiation is wrong, and that whether a half-egg shall develop into a whole animal or a half-animal, depends simply upon its relation to the other half. If in contact with the other half it develops only half of the adult structure, while, if separated by itself it may develop a whole animal. Such results would, of course, suggest that the development is dependent upon relations and not upon the unfolding of some germ structure already present in the egg. When experiments give such contradictory data it is, of course, difficult to draw any conclusion, but the general opinion of students to-day is, that Weismann's conception of the gradual unfolding of

the germ plasm during development is not in harmony with the facts.

There are other lines of experiments directed toward the solution of similar questions. We have learned that the hereditary characters are in the egg nucleus, and that in fertilization this unites with another nucleus from another (male) individual. Experiments are devised depriving an egg of its nucleus and substituting a nucleus from some other source, and then watching the development to see whether the new nucleus or the original egg substance most controls development. Or, again, the egg is deprived of its own nucleus and two nuclei are supplied to it from two male cells, to produce an individual with two father nuclei instead of one father and one mother nucleus. Or, again, two egg nuclei are introduced into an egg instead of a male nucleus. In a different line equally significant experiments are made to test how far development may be modified by changes in the conditions. Eggs are placed in water containing an extra amount of salt, or an extra amount of other chemicals. Eggs which develop lime skeletons in the early embryo are placed in water containing no lime, or an unusual amount of lime. Eggs are forced to develop at unusually low or high temperatures. More extraordinary still are experiments which have shown that eggs which normally require fertilization may be stimulated to develop without union with a male cell, by simply treating them with certain simple salts. All such experiments tend, of course, to give information in regard to the influence of

external agents upon development, and thus indicate to what extent the adult is the result of a simple unfolding of the structure of the egg and to what extent it may be made up of acquired characters developed by the direct action of the environment.

Similar lines of experiment are carried on with adults which have the power of reproducing lost parts. Most plants can replace lost members, and this is also true of many lower animals. Such phenomena offer suggestive questions bearing upon the structure and the powers of protoplasm. When, for example, a lizard reproduces a lost leg, does he do this in a similar manner to that in which the original leg was produced, and hence under the influence of similar forces and perhaps similar germ plasm stored away in the body cells, or is the new leg developed in a different manner and therefore under the influence of a new set of forces? Weismann, in accordance with his idea of the structure of the germ plasm, assumes that in the body cells there is present some partly differentiated germ plasm which immediately takes charge of the process of redeveloping the leg; while the opposing school must give a different explanation. When certain amphibia are deprived of the lens of the eye they will develop a new one in a short time. But in this case it has been found that the new lens is produced in a manner entirely different from the first lens. Originally the lens is developed from the ectoderm, or outer skin, while the new lens develops from the edge of the iris, which is a part of the mesoderm, an entirely different part of the body. Here we are seemingly

forced to abandon Weismann's view of germ-plasm differentiation, and to insist that there is some agency superior to the germ plasm that controls the results. The parts of the eye act almost as if they were intelligent, and when a lens is lost and cannot readily be developed from the ectoderm in the original manner, the other parts take upon themselves the duty of producing a new lens. Without, however, dwelling upon the results, they will serve our purpose of illustrating the sort of experiments that are undertaken by this new branch of biological science in its attempt to learn something about the structure of protoplasm and the forces engaged in producing the development of organisms. Naturalists occupy a position to-day somewhat akin to that of the chemist before the formulation of the atomic theory.

It would be entirely out of place to try to summarize the results. In the first place they are not yet in agreement. Even the simple experiments do not always produce the same results. Contradictions occur on all sides, and how far these are due to imperfections in methods, and how far to differences in the actual nature of different animals, cannot yet be stated. Observations are multiplying, but the whole subject is still too confusing to make it possible to draw any very valuable general conclusions. The line of research is a difficult one. The experimenting requires great ingenuity in performing, and great care in interpretation. Results cannot be expected at once. The study of the changes which take place in the division of the cell required many

years of observation before they were understood. So in this new line of study we can hope for valuable lessons only after much more extended observation.

The object of bringing up the matter here is not, therefore, to give any conclusions bearing upon the method of the origin of species, but simply to point out the new lines of investigation which modern biologists are following in their endeavor to solve the problems of heredity and variation. What the results of this field of attack may be in the future cannot be surmised, but it is certainly a promising line of study. It is a line of research that is to-day attracting the attention of many of our best naturalists, and especially of the younger men, who feel that there is little hope of progress along the road of speculation and discussion that has occupied biologists since Darwin. Perhaps this new department of experimentation may lead to the discovery of some of the unknown forces which naturalists tacitly acknowledge must be discovered before we can rest satisfied with the conclusion that we have solved the method of the origin of species. Up to the present, however, none of these studies have yielded results which throw much light upon the method of the origin of species.

### *General Summary*

It may serve to make the subject a little clearer if we give in conclusion a general summary of the present attitude of science toward the question of

the method of evolution. Such a summary may, doubtless, be open to criticism and revision in details, but its general content will not be far from expressing the present attitude of naturalists toward the subject.

The production of our modern species of animals and plants has been dependent, in the first place, upon the property of reproduction, a property that is universal with life. It is a function of protoplasm and is at present unintelligible to us. This power of reproduction belongs to three different grades of living matter: first, to individuals, second, to the cells or minute parts out of which the individual is composed, and, third, to the still more minute elements out of which the cell is composed, which have been called plasms. Each of these grades of organized matter plays its part in the production of species.

This protoplasmic substance appears to have been absolutely continuous from generation to generation, simply being handed on from parent to child, but ever increasing in amount. Of its origin we know nothing except that, being a mechanism, it could never have been produced by purely chemical forces. The evolution of the organic world and the origin of species has been due to the gradual changing of the characters of this substance.

In all organisms above the lowest we find that the individual is made up of thousands of more or less independent parts called cells, and that a single *one* of these cells is set apart to produce the next generation. Moreover, we have abundant reason for

believing that there is a certain part of this reproductive cell which actually controls the development of the next generation, and this substance is handed on from generation to generation and serves as a continuous basis for the development of successive generations. We call it "germ plasm," and we come thus to distinguish two quite different phases of living matter. The one is this germ plasm, which is continuous from age to age; the other is the individual that carries the germ plasm, and that exists only for a short time, dying and disappearing after producing other individuals for carrying the germ plasm. This individual constitutes the species as we see it, and it is this individual that we are trying to explain in the study of the origin of species. Whether the germ plasm is distributed through the body of the individual or only in its reproductive cells, whether it is distinct and independent from the protoplasm that is in the body cells and controls the life of the individual, are questions of theoretical interest not yet settled. It is, however, universally agreed that there is something that is continuous from age to age, and forms the basis of the reappearance of like individuals in successive generations.

In the individuals that appear in successive generations we see two somewhat opposite tendencies. We find, first, that they show a very decided tendency to be alike, a feature which we speak of as *heredity*. Second, we see that they also show a tendency to be unlike, and this we speak of as *variation*. Clearly these variations may be of two

different kinds. Some of them may appear in this continuous germ plasm, and when this occurs the variations in question will be handed down to later generations, since the germ plasm is handed on from age to age. Others may occur in the individual as the direct result of the action of the environment upon it. When the body dies they naturally disappear, unless in some way they have impressed themselves upon the germ substance. Whether they can do this is still a question, but since they may be redeveloped in each generation so long as the same environment acts upon a similar germinal substance, they will *constitute a part of the specific characters* whose origin naturalists are trying to explain. The origin of species must include, therefore, both acquired and congenital characters.

These variations constitute the building stones out of which the species of animals and plants have been built, and evolution has occurred by the accumulation of these variations one upon another in successive generations. As to the cause of the variations, our knowledge is still very inadequate. Some of them are due probably to the general instability of protoplasm and germ plasm; some to the direct action of a changing environment upon the living substance, and some, perhaps, to the result of the mixture of germ plasm from different sources in the process of sexual reproduction. The variations are very generally of a slight extent and simply to be looked upon as departures from a general average, since all characters, roughly speaking, will be arranged half above and half below the average.

Such variations are universal. But, in addition, there are frequently variations of a greater extent, called discontinuous variations. They consist in the sudden and wide departure of any individual from the type of its parents, due to some forces acting upon the germ plasm, which we do not understand. But such variations do occur and are actual factors in the evolution of species.

The force by which these building stones have been put together to make different species, producing the evolution of organisms, has been chiefly selection. Selection is one of the most universal forces connected with organic life and it acts upon acquired and congenital characters alike. Selection simply means that in some way certain varieties have an opportunity of leaving offspring, while others have no such opportunity. But there are various kinds of selection. In the breeding of domestic animals and plants, selection is the choice of the breeder. Only the types which he chooses have the opportunity to reproduce, and they, of course, thus control the future development of the race. In nature, other forces take the place of this choice. Foremost among them stands natural selection, a force which brings it about that, among the numerous varieties, it is only those that are best fitted for the conditions that survive the severe struggle for existence which over-production brings about. The result is that the survivors will always be from among those the efficiency of whose organs to adapt them to their conditions is above, rather than below, the average. The second generation will

thus be descended from parents whose ability to contend with conditions is somewhat above that of the average of the first generation. So far as the variations are in the germ plasm, they will be inherited, and thus a step in advance is taken by the elimination of the individuals least able to cope with conditions. This survival of the fittest little by little builds up organs and produces the adaptation which is the marvel of nature. The race thus advances, generation after generation, with a broad front upon the principle of the survival of those the sum of whose characters, congenital and acquired, stands above the average of efficiency. But, although this is the rule, it is, on the other hand, pretty clear that occasionally a discontinuous variation starts a new line of descent. By means of it a large addition to the structure is sometimes made at a single step.

But such an advance, by the slow accumulation of slight steps, would tend to carry all of the animals of a species together along the same line. Free cross-breeding of the individuals of any species will prevent any great departures from the average. Discontinuous variations would naturally be eliminated by crossing, and no divergence of two or more lines of descent would be produced by natural selection acting upon averages. But there has been in the history of evolution a variety of forces which have tended to separate groups of animals from their allies, so far as concerns inter-breeding, and this isolation at once tends to break up the descendants of any species into

groups. The forces that produce this segregation are varied, including geographical and physiological, as well as social and mental factors; but the result is the close inter-breeding of the members of isolated groups. This causes each group to develop in a line by itself and thus produces divergent evolution. By such segregation the descendants of a single species are separated from each other, and then, by the accumulation of variations in different groups, each begins to travel in a line somewhat different from the other. In time the two groups become distinct species. By isolation and selection, then, species have continually changed and become ever more diversified.

The most prominent question before biologists has been, and still is, in regard to the relation of the two types of variation. Plainly, only such variations as affect the germ plasm can permanently influence evolution. But do these variations always originate in the germ plasm or may they arise first in the body and then be transferred to the germ? Do variations in the body count permanently, or only temporarily—for each generation? It is still unsettled whether variations appearing in the body of an individual, after the fertilization of the egg, actually become incorporated into the germ plasm so as to be inherited, although it is almost certain that something of this sort does occur, at least in plants. But whether this is so or not, such variations certainly play a very important part in the process. First, it appears that many of the characters of our present species are not matters of heredity at all,

and hence are not necessarily expressed in the germ plasm. They are simply acquired independently by each generation as the result of the action of external forces upon the unstable protoplasm. We call them "specific," since they are universal with the species, but they are not necessarily inborn. So far as specific characters are of this nature they are, of course, "acquired" rather than "congenital." But it is these acquired characters which adapt the individual directly to its conditions and thus enable the animals and plants to adopt new habits when the necessity arises. Were it not for them, organisms would have a hard time of it. If it were necessary for an animal or plant to wait for an appropriate accidental variation in the germ plasm before it could adopt new habits, evolution could hardly advance at all. But these acquired characters enable the individual to be directly adapted to its conditions and shield it from destruction until some fortuitous variation may later arise in the germ plasm which is of use in the particular conditions of life. This is then selected by natural selection and is thereafter transmitted as an inherited trait, since from the first it has been part of the germ plasm. Thus acquired characters play a very important part, guiding the course of evolution, whether or not they are directly inherited.

These various forces acting together produce organic evolution. A species of to-day is thus the result of the selection of certain variations occurring in the germinal substance, combined with others that have arisen in the body cells as the result of

external forces. The exact relation of these two types of variation to each other may not yet be satisfactorily settled. Neither Neo-Lamarckism, which bases evolution chiefly upon acquired characters, nor Neo-Darwinism (Weismannism), which bases it entirely upon the natural selection of congenital characters, is wholly satisfactory. Each type of variation certainly plays a part in the animals and plants as we see them to-day. The accumulation of congenital variations combined with, or at least aided by, acquired variations, has produced phylogenetic variation, or the evolution of the organic world.

There are many points in the process in regard to which we are still in darkness. That the actual process of species building has been by the selection of variations which have become incorporated in the germ plasm, seems certain enough. The method of the construction of the species out of the building material, *i. e.*, variations, we think we understand tolerably well. But as concerns the material out of which the species is constructed we have little knowledge. The nature and cause of variations, the question whether they are wholly fortuitous or whether they occur in lines determined by some more fundamental unknown force, whether they are adapted to their purpose before selection or whether the adaptation comes only because of selection, whether there are yet unknown forces which determine the reappearance of similar variations in many individuals at once and for many generations, all these are questions still unanswered. Their answers

are plainly to be found along the lines of the study of variation and protoplasm, if they are to be found at all. These two topics are, therefore, the ones which present day naturalists are eagerly investigating in the hope of being able to throw light upon some of these places which are yet shrouded in darkness. The study of variation is showing us how natural selection really acts in the world, it is disclosing the significance of discontinuous variations as well as minute variations, and is possibly disclosing the appearance of variations along determinate lines. The study of protoplasm has already shown this substance to be a mechanism, demanding, therefore, a solution from mechanical rather than chemical forces. It has shown us a marvellous complexity and a wonderful activity concealed even in the simplest life substance. Lastly, the study of developmental mechanics is apparently proving that external forces have considerable influence upon the characters of the adult, and that, therefore, the method of evolution which has been adopted by nature involves something besides the gradual modification of germ plasm.

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